Cognitive Mechanisms and Geophysical Factors Influencing Navigation in Homing Pigeons (*Columba livia*)

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∞ *I dedicate this work to my family* ∞

Content

Zusammenfassung

Die Fähigkeit eines Vogels sich über hunderte oder tausende Kilometer zu orientieren ist eine erstaunliche Leistung, weil das Navigieren in unbekannten Gebieten mit zahlreichen Schwierigkeiten verbunden ist. Durch die Einkalkulierung von internen und externen Informationen wird die Navigation zu einer sehr komplexen Aufgabe. Es wurde bereits eine Vielzahl von unterschiedlichen Theorien zu Navigationsstrategien veröffentlicht, um die verschiedenen Mechanismen der Navigation zu erklären. Die im Jahre 1957 entwickelte Karte-und-Kompass-Strategie von Professor Kramer hat in der Forschung eine grosse Akzeptanz gefunden. Darin wird festgehalten, dass Tiere zuerst ihren eigenen Standort (Karte) und dann eine Richtung (Kompass) bestimmen, um ihren Navigationskurs festzulegen. Es ist ein zweistufiges Vorgehen, das einen 'Kartensinn' und einen 'Kompasssinn' voraussetzt. In Studien wurde ersichtlich, dass die Vögel eine Vielzahl von Richtungsreferenzen wie Seh-, Hör- und Geruchssignale aus ihrer Umwelt für ihr Navigieren nutzen. Die Brieftauben verwenden beispielsweise die Nord-Süd-Achse des Erdmagnetfeldes und die Laufbahn der Sonne. Zudem orientieren sich migrierende Vögel am Rotationsmuster der Sterne. Über die Mechanismen der genauen Standortbestimmung und welche Informationen die Vögel benutzen, um ihren momentanen Ort zu bestimmen, ist hingegen wenig bekannt. Bisher wurden Infraschall, Erdmagnetfeld und Geruchssignale als mögliche Faktoren für den Kartensinn der Vögel in Betracht gezogen. Jedoch sind bis heute diese möglichen Orientierungshinweise noch nicht adäquat getestet worden und ferner besteht noch Zweifel, ob sie als Referenzen für einen Kartensinn gelten. Das wissenschaftliche Belegen und Erläutern des sogenannten Kartensinns ist demzufolge noch immer ein ungelöstes Problem in der Erforschung der Vogelnavigation.

Das Ziel dieser Dissertation ist es, die unterschiedlichen Konzepte und Theorien des Kartensinns der Brieftauben zu untersuchen und zu überprüfen. Zuerst wurde untersucht, ob Brieftauben womöglich eine kognitive Karte besitzen. Zu diesem Zweck wurden die Brieftauben trainiert zu einem 27km weit entfernten Futterkäfig zu fliegen. Dadurch sollten sie zwei mögliche Zielkoordinaten, den Heimschlag und den Futterschlag, gespeichert haben. Danach wurden die Vögel an einem ihnen unbekannten Ort freigesetzt, der die gleiche Distanz zu beiden Schlägen hatte. Die eine Hälfte der

Gruppe erhielt Futter vor der Freisetzung, während die andere Hälfte hungrig blieb. Für die Standortbestimmung beim Abflug wurde bei den vier Studien in der Schweiz mit Verschwinderichtungsmethoden gearbeitet. Dabei wird das Verschwinden eines Vogels aus dem Sichtfeld eines Beobachters mit einem Feldstecher gemessen und notiert. In Italien wurde eine zusätzliche Studie durchgeführt, bei der die Tauben mit GPS-Geräten ausgestattet wurden und somit der gesamte Flugverlauf aufgezeichnet werden konnte. Nach der Freisetzung starteten die hungrigen Tauben ihren Flug mit Zielrichtung Futterschlag, während die gesättigten Tauben nach Hause flogen. Diese Resultate implizieren, dass sich die Tauben aufgrund ihrer Motivation und der Berechnung ihrer Position vor Ort in Bezug zu den zwei gespeicherten Schlagorten für eine Flugrichtung entschieden. Demnach müssten sie Kenntnis über ihre Position im Verhältnis zu den anderen Zielorten gehabt haben. Das ist das Wesentliche einer kognitiven Karte. Zusätzlich bestätigen die Resultate auch, dass Brieftauben eine Karten-und-Kompass Strategie benutzen und somit wird der alleinige Gebrauch von einfacheren Strategien, wie z. B. das Folgen von sensorischen Signalen zum Heimschlag, als einziger Referenzpunkt verworfen. Den Rückweg nach Hause kann der Vogel auch ohne mentale Karte bewerkstelligen, aber unterschiedliche Ziele zu finden erfordert höhere kognitive Prozesse.

In einem zweiten Schritt haben wir eine noch unbeachtete Theorie über die Vogelnavigation getestet. Die Theorie, die von V. Kanevskyi im Jahre 1984 aufgestellt wurde, besagt, dass navigierende Vögel auf den lokalen Schwerevektor des Geburtsorts geeicht werden, analog zu der Funktionsweise eines mechanischen Gyroskops. Ein Gyroskop bewahrt die Anfangsorientierung des Schwerevektors durch die schnelle Rotation verschiedener Räder in unterschiedlichen Ebenen. Durch den Vergleich des gespeicherten Heim-Schwerevektors mit dem wahrgenommenen Schwerevektor am momentanen Aufenthaltsort können Vögel die Distanz und die Richtung nach Hause berechnen und navigieren demzufolge nach einem polaren Koordinatensystem. Diese Theorie bedarf einer Überprüfung, bevor man im Vogel nach neuronalen Korrelaten eines Gyroskops sucht.

Da der Schwerevektor in Feldstudien experimentell schwierig zu manipulieren ist, wurden Regionen gesucht, in denen eine natürlich vorkommende Neigung des Schwerevektors existiert. In Randzonen von Schwereanomalien, die aus unterirdischen Anreicherungen von Material mit hoher oder geringer Dichte gebildet werden, wird der Schwerevektor horizontal geneigt (Neigung des Schwerevektors = horizontaler Schweregradient). Solche Ablenkungen könnten die Brieftauben im Orientierungsprozess möglicherweise irritieren.

Wir führten zwei verschiedene Experimente mit GPS-Geräten durch: In einem der beiden Experimente wurde der Einfluss der Richtung des Schweregradienten in einer Schwereanomalie auf die Aufzucht der Tauben untersucht. Wie die Schwerevektortheorie voraussagen würde, waren die Tauben besser orientiert, die auf einem Schweregradienten aufwuchsen, der mit der Heimwärts-Richtung übereinstimmte, als diejenigen Tauben, die auf einem Schweregradient aufwuchsen, der sich rechtwinklig zur Heimwärts-Richtung befand. Eine zweite Voraussage der Theorie war, dass Tauben schlagartige Veränderungen in ihrem Flugkurs aufzeigen würden, sollten sie Schwereanomalien überfliegen. In der Tat veränderten ein paar Tauben ihren Flugkurs abrupt und flogen mehrere Bogen innerhalb der Anomalie. Da magnetische Anomalien oft mit Schwereanomalien vorkommen, wurde die geomagnetische Variation in der Region ebenfalls untersucht. Die Orte der Taubenschläge waren frei von geomagnetischen Anomalien und die Flugpfade schienen sich mehr nach den Schwereanomalien zu richten als nach den Magnetanomalien.

Im zweiten Experiment wurde der Einfluss von Schwereanomalien ohne das Vorkommen von Magnetanomalien auf die Taubennavigation getestet. Dafür wurden Brieftauben, die unter normalen Schwerefeld- und Magnetfeldbedingungen aufgezogen worden sind, innerhalb und hinter einer starken kreisförmigen negativen Schwereanomalie freigelassen. Diese Anomalie ist durch einen Meteoriteneinschlag verursacht worden und äussert sich durch eine grosse Neigungsänderung des Schwerevektors in den Randzonen der Anomalie. Eine Gruppe von Kontrolltauben wurde aus gleicher Entfernung zum Heimschlag freigelassen (91km), doch ohne das Vorkommen von Anomalien auf der geplanten Route. Wie erwartet von der Schwerevektortheorie flogen beide Gruppen in die Heimwärts-Richtung. Allerdings veränderten viele Tauben ihren Flugkurs, nachdem sie die Randzone der Schwereanomalie überflogen hatten. Überraschenderweise behielten die Tauben den abweichenden Kurs über längere Entfernung bei, wohingegen die Kontrollvögel sich auf einer direkten Linie dem Heimschlag näherten mit der Ausnahme von drei Tauben, die auf eine zweite Schwereanomalie trafen und ihren Flug abrupt änderten. Folglich unterstützen beide Anomalien-Experimente die Schwerevektortheorie und machen den Gebrauch des Schwerevektors bei der Standortbestimmung bedeutend. Mit der Standortbestimmung können die Brieftauben mit Hilfe von Kompassreferenzen navigieren, hauptsächlich indem sie die Karten-und-Kompass-Strategie mit periodisch aktualisierten Positionsbestimmungen gebrauchen. Für migrierende Vögel wäre eine Standortbestimmung aufgrund des Vergleichs der Schwerevektoren ein wichtiger globaler Mechanismus, um die eigene Position während

der Migration zu lokalisieren. Die Forschungsergebnisse dieser Dissertation leisten einen wertvollen Beitrag zum heutigen Wissenstand der Navigation der Brieftauben, indem sie eine etablierte Theorie bestätigen und eine neue, noch unbeachtete Theorie überprüfen konnte.

Summary

A bird's capability to navigate over hundreds or thousands of kilometers is truly an astonishing accomplishment. True navigation in unknown regions requires computation of internal and external information, a complex task explained by different theories on navigational strategies. Among them, the map-and-compass strategy formulated by Kramer in 1957 has found broad acceptance. It postulates that birds determine their position (map) and a direction (compass) in order to set a flight course. This is a two-step procedure that prerequisites a 'map-sense' and a 'compass-sense'. Studies have revealed the use of a multitude of directional references provided by visual, auditory and olfactory cues from the environment. For long-distance navigation, pigeons use the north-south axis of the earth's magnetic field and the sun's orbit. Migratory birds use in addition the rotational pattern of stars. However, little is known about the mechanisms of position-determination and the references that could provide the bird with positional information. Until now, infrasonic waves, the earth's magnetic field and olfactory cues have been proposed to contribute to the map sense of birds. However, those references have either not been tested adequately or are doubted to function as a reference for a map. Thus, the map sense remains an unsolved problem in the investigation of bird navigation.

This thesis aims at testing concepts and theories of the map sense of homing pigeons. Firstly, we investigated whether pigeons have a cognitive navigational map. To this end, pigeons were first trained to fly regularly 27 km to a distant food loft and back so that they had two potential target coordinates in mind: the home and the food loft. We then released the birds, half of them were hungry and the other half were fed, from an unknown area equidistant to both target lofts. We used vanishing bearing methods recording the vanishing of a departing bird with binoculars in four releases in Switzerland. In Italy, we conducted an additional study using pigeons equipped with miniaturized GPS-loggers to record their flight tracks. Already at departure, the hungry pigeons set a course toward the food loft and the fed pigeons headed toward home. The findings implicate that the pigeons could compute a compass course from their actual position to two memorized locations depending on their motivational state. Thus, they must have had knowledge of their position in relation to the other two targets. This is the essence of a cognitive map. In addition, the results also confirmed that pigeons

use a map-and-compass strategy and reject an exclusive use of simple strategies reducing the difference of sensory cues to the home loft as the only navigational reference point. Finding home can be achieved without a mental map, but finding different targets requires higher cognitive processes.

In a second step, we tested a neglected theory about bird navigation. Formulated by Kanevskyi in 1984, the theory holds that navigating birds become imprinted to the local gravity vector at their birth place. This home gravity vector is being memorized analogous to the workings of a mechanical gyroscope that maintains the orientation of the gravity vector at the starting point by means of wheels spinning at high speed. By comparing the memorized home gravity vector with a sensed gravity vector when the bird is far from home, the birds can calculate the distance and direction to the home loft, thus navigating according to a global polar coordinate system. This theory requires verification before searching for neuronal correlates of a gyroscope within a bird.

As the gravity vector is experimentally difficult to manipulate in field studies, we searched for regions with naturally occurring inclinations of the gravity vector. Such inclinations are found in the border zones of gravity anomalies caused by subterranean deposits of high-or low-density material, which bend the gravity vector horizontally (inclination of the gravity vector = horizontal gravity gradient). These deviations could potentially irritate homing pigeons when navigating home.

We conducted two different experiments with GPS loggers: in one experiment, we investigated the influence of rearing pigeons on gravity anomalies where the gravity gradient (inclination of the gravity vector) showed different orientations. As predicted by the theory, pigeons that were raised on a gravity gradient coincident with the home direction from a test release site were better oriented than pigeons raised on a gravity gradient perpendicular to the home direction. A second prediction of the theory was that pigeons crossing gravity anomalies should show sudden changes in their flight paths. Indeed, GPS-tracking of crossing gravity anomalies often but not always showed more tortuous flight paths and some pigeons changed their flight course abruptly within the anomaly. Since magnetic anomalies are often associated with gravity anomalies, we investigated the geomagnetic variation in the region. The loft sites of the pigeons were free of geomagnetic anomalies, and flight tracks appeared much better aligned with gravity anomalies than with geomagnetic anomalies.

A second experiment was conducted to test specifically whether gravity anomalies not associated with magnetic anomalies could show comparable effects on pigeon navigation. Pigeons that were raised under normal gravity and magnetic conditions were released from the center and from behind

a large circular negative gravity anomaly. The gravity anomaly was caused by a meteorite impact that entailed a large change of the gravity gradient in the border zones of the anomaly, devoid of magnetic anomalies. A group of control pigeons was released from outside the anomaly at the same distance from the home loft (91 km). As anticipated by the theory, both groups of pigeons departed initially well homewards. However, many pigeons released from the center and behind the anomaly changed their course after having passed the border zone of the anomaly. Intriguingly, these pigeons maintained a wrong flight direction over long distances, whereas the birds released from the control site converged their flight paths successively toward the home direction, with the exception of three pigeons that flew into a second gravity anomaly where they altered their flight paths abruptly. Thus, both gravity experiments provided substantial support for the gravity vector hypothesis, and it seems probable that pigeons use the gravity vector as a position-finding mechanism. Pigeons might also include compass references to navigate home, chiefly by using a map-and-compass strategy combined with periodical position fixes. For migratory birds, a map sense based on the comparison of gravity vectors would be an important global mechanism to locate their position during migration. The findings of this thesis add valuable information to the knowledge of pigeon homing and navigation by confirming established theories and by verifying a novel navigational theory.

Introduction

General background of homing pigeon research

Animal movement is one of the fundamental characteristics of life. Specifically animal migration, the seasonal and geographical variation of animal populations, has an enormous impact on ecosystems and evolutionary processes (Baker, 1978). There are billions of animals migrating each year according to temporal changes to their habitat. There are daily vertical movements of zooplankton (Hansson et al., 2009), seasonal migration of 4000 km of monarch butterflies over several generations (Brower et al., 2006) and crossing of the Himalayas at 6000 m of bar-headed geese (Hawkes et al., 2011). The fascination of animal movement has caught philosophers' interest as early as the 4th century B.C. when Aristotle searched for common features unifying animal movements.

Among the best migrating animals are birds. Migratory birds have an extraordinary capability of flying great distances and returning to the same breeding site year after year (Berthold et al., 2003). The arctic tern travels between the arctic and the Antarctica, a distance of up to 80'000 km each year (Egevang et al., 2010). The prerequisite for such an achievement is not only the physical ability to fly these distances but also their navigational ability to orient over long distances. An outstanding example of navigating over a 'featureless' ocean is the wandering albatross *Diomedea exulans*. It takes foraging trips of several of thousands of km in the Southern Indian Ocean from which it returns precisely to its colony (Jouventin et al., 1990, Bonadonna et al., 2005). This impressive navigational ability of birds has led to an increased investigation of the mechanisms and the sensory basis of orientation and navigation in bird migration and homing. The term 'navigation' can lead to some confusion as it is used differently in various contexts. In bird research, the term is commonly defined as 'true' navigation which means navigating in unfamiliar terrain as opposed to flying in areas birds have been before. This is a crucial distinction insofar as navigating in an unknown area requires other navigational abilities than flying in a familiar region. On the other hand, homing is generally referred to an animal moving from a distant position to its nest or breeding grounds without making any assumptions on the familiarity of the homing area.

Research on the navigational abilities of birds has predominantly been conducted with homing pigeons for good methodological reasons (Wallraff, 2005): they are handy in size, can be kept in aviaries and return almost always home, are all-year available, very robust and easy to handle. Homing pigeons are domesticated pigeons, descendants of the wild rock pigeon. They have been bred for different phenotypes and purposes since thousands of years. For scientific research, homing pigeons serve as an animal model of bird navigation. Therefore, over the past half a century, almost all experiments aiming to unravel the mystery of navigation have been conducted with homing pigeons. True navigation has been found to exist in homing pigeons and migratory birds. First-flight homing pigeons could home when released 300 km distant from their home loft (Wallraff, 1986), and more experienced pigeons were able to fly over 600 km from Germany to Italy (Ioalé et al., 1983). Long-distance races of pigeon breeder associations cover distances from Barcelona to Belgium. As for migratory birds, displacement studies can show true navigation as in the case of a study where reed warblers were captured in Europe and transported by plane 1000 km to the east: the birds adjusted their orientation according to their displacement (Chernetsov et al., 2008).

One of the cornerstones in navigation research is the two-step map-and-compass theory formulated by Kramer (1953, 1957). Kramer proposed that animals orient first by determining their position (map-step) and then by setting a direction (compass-step). The orientation process therefore can be divided into two distinct tasks. As a consequence, researchers have focused on either investigating the map- or the compass-step.

The compass

Possible compass cues implied in the orientation process have been easier to detect in past studies and therefore remain the most investigated aspect of the two-step theory. Kramer commenced investigating the role of the sun in 1950 that has lead to a series of experiments. As the sun's position changes over time, birds need to compensate that shift with their internal clock. Schmidt-Koenig (1958, 1960) conducted experiments with pigeons that experienced a day-night cycle shifted by 6 hours. When releasing the clock-shifted pigeons, their initial orientation deviated by roughly 90° according to the calculation of the sun's position with their inner clock. In addition, the birds did not calculate the altitude of the sun but instead the azimuth, which is its angular position along the horizon. Summarizing these early findings, the most recognized compass cue in the orientation process is a time-compensated sun-

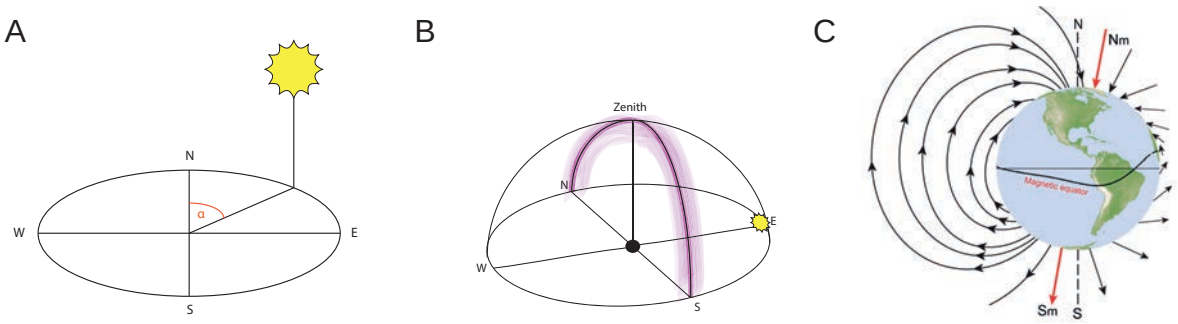

Fig. 1. Different compasses used by birds. A) The azimuth of the sun, indicated by the red angle α. B) A polarized light band at sunrise, indicated by the violet line. C) The earths' magnetic field. The field lines are shown an the left and the inclination angles are apparent on the right. The red arrows show the magnetic poles. Nm = magnetic North pole. Courtesy of Prof. D. Dickman [1].

azimuth compass (Fig. 1A). A decade later, Emlen (1970) exposed indigo buntings to a planetarium sky in which the stars' rotation could be manipulated. Indigo buntings that were prevented from sight of the stars did not show a normal migratory direction. Indigo buntings that were exposed to a wrong axis of rotation exhibited the 'correct' migratory direction in accordance to the axis of rotation. Thus, the axis of celestial rotation provides the birds with a directional reference system.

The earth's magnetic field is another possible candidate for compass orientation. The earth's magnetic field has a clear north-south-axis with corresponding changes of the magnetic field intensity (low at equator, high at poles) and the inclination angle (0° at equator, 90° at poles, Fig. 1C). The first study on magnetic orientation was conducted with European robins, Erithacus rubecula, that were placed in a laboratory where magnetic conditions were manipulated (Wiltschko, 1968). The robins changed their orientation according to the magnetic north rotated by coil systems. However, the bird's orientation did not change when the inclination angle was kept stable and the polarity was inversed (Wiltschko et al., 1972). These findings implied that the magnetic compass is an inclination compass based on the intensity field lines and the inclination angle but not on the polarity of the earth's magnetic field. In homing pigeon research, Keeton provided the first indication for magnetic compass orientation in homing pigeons (1971). It has been suggested that the magnetic inclination compass is a widespread phenomenon as it has been found in various migratory birds species (Able, 1994, Wiltschko et al., 1996).

Another environmental cue used to derive directional information is polarized light (Fig. 1B). Able (1982) manipulated the axis of skylight polarization, which changed the migratory orientation of the white-throated sparrow Zonotrichia ablicolllis. Detection of polarized light was also found in homing pigeons (Kreithen et al., 1974) bur further studies revealed no sensitivity of homing pigeons

to polarized light (Coemans et al., 1994).

While the nature of (some) compasses was identified, the question arose whose preference the bird would give in what situation and which compasses might be calibrated by others. Studies on conflicting directional information from two or more cues were conducted to answer the problem regarding the use of polarized light and the magnetic field (Muheim et al., 2006a). Muheim and colleagues showed that migratory Savannah sparrows recalibrate the magnetic compass by using polarized light cues at sunrise and sunset (Muheim et al., 2006b). Therefore, they concluded that the prime calibration reference were polarized light cues near the horizon at sunrise and sunset for migratory songbirds. When the sun is visible it is clearly dominant over magnetic information. However, the magnetic compass may play an important role when clock-shifted pigeon return home (Wiltschko et al., 1996). Also, according to Wiltschko et al. (1981), young pigeons use first a magnetic compass before they learn to apply a sun compass. In general, experiments under overcast skies are inconsistent in their findings and thus a firm conclusion cannot be drawn (Wallraff, 2005).

The map

The map-step of Kramer's theory has remained the more difficult to investigate and until now, the sensory basis of the map-step is still unknown. The map-step is also more challenging in terms of conceptualization. There are different theories on how maps could function also in view of the underlying implementation of environmental information. There is a clear distinction of maps that are built according to experience, involving the use of familiar visual, olfactory or magnetic cues. These maps are referred to mosaic maps, familiar area maps or topographical maps in which the previously experienced information and their spatial relation is stored and retrieved when needed. Since true navigation is referred to homing from unfamiliar places I will not present the extensive research on homing from familiar places (Holland, 2003, Bingman et al., 2005, Gagliardo et al., 2009). Instead, I will focus on studies that show how birds navigate home from unknown regions.

The concept of a map used in unfamiliar areas is a grid map. A grid map consists of at least two variables that vary systematically in different directions over large regions, so-called gradients of different physical nature. Ideally, each site would be represented by a unique combination of coordinates (Fig. 2A). The grid must be learnt at the home site by recognizing increasing and decreasing values but then could theoretically be extrapolated to unfamiliar regions. At the release site, the pigeon could

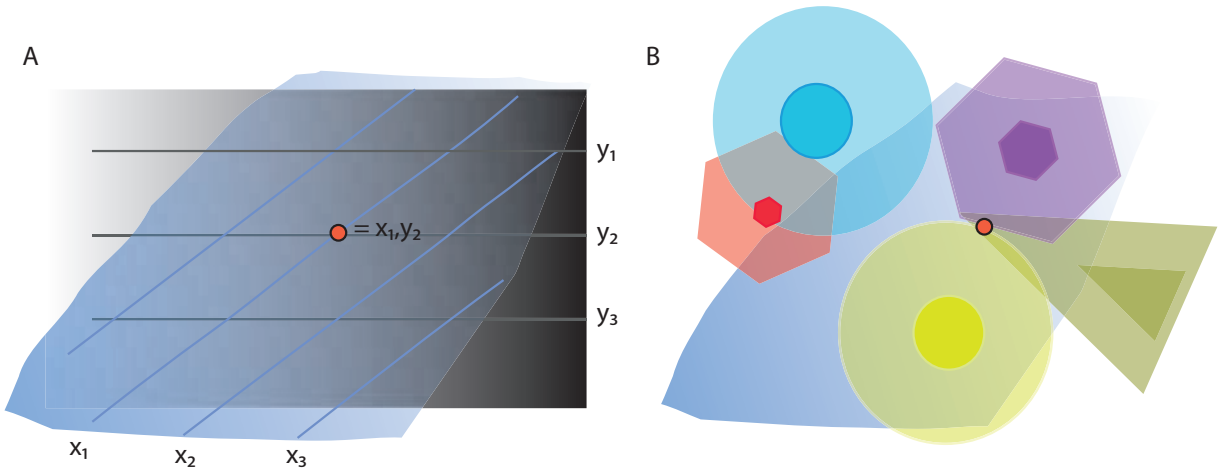

Fig. 2. Concepts of maps. A) Grid map formed by two intersecting gradients, x and y. Extendable to distant places. B) Mosaic map formed by cues in a spatial arrangement. Limited in range. The orange dot indicates the position of an animal.

compare the perceived values with the remembered values from home and estimate its position. This information can then be used for two types of homing strategies. The first fits the map-and-compass principle. The pigeons calculate the direction and the magnitude of the differences, from which they can deduct a home direction and the approximate distance. This requires a minimum of cognitive operations, including the ability to establish a mental map holding the own and the loft's position. The alternative strategy is that the birds simply try to minimize continually the differences between the various gradients until they arrive at home where there is no difference. This largely non-cognitive strategy is technically known as "zeroing-in". For pigeons, it has proven difficult to distinguish between such navigational strategies, but the present thesis includes a chapter showing that pigeons are able to fly according to a cognitive map-and-compass strategy.

Olfaction has been demonstrated to be a crucial sensory modality for pigeon homing. Papi initiated research on the involvement of the olfactory system on homing by cutting the olfactory nerve of pigeons (1971). A variety of experiments followed in depriving the bird from olfactory access by anesthetizing the nasal mucosa (Ioalé, 1983, Wallraff et al., 1984, Benvenuti et al., 1989), plugging the nostrils (Snyder et al., 1975) and inactivating the olfactory epithelium by zinc sulphate (Benvenuti et al., 1992, Gagliardo et al., 2000, Bingman et al., 1998). The applied methods differ in various aspect, however a general conclusion can be drawn, that olfactory deprivation led to great losses, poor initial homeward orientation and low homing speed compared to controls. But the application of airborne chemical cues in navigation is still debated heavily. The most frequent arguments are that the invasive methods might disturb other sensory systems (Wiltschko, 1996, Walker 1999, Mora

et al., 2004), or that olfaction might play a role in activating navigation instead of being part of the navigation process itself (Phillips et al., 2006, Jorge et al., 2009). In addition, other aspects such as the temporal variability, the influence of temperature on volatile compounds, varying wind directions, spatial continuity and our lack of knowledge of the nature of perception of chemical compounds make the acceptance of the olfactory map hypothesis difficult.

Conceptually, Papi has suggested that pigeons can learn odors or combination of odors from different sources transported by winds, forming a "mosaic map" (1972). Like distant landmarks, the pigeons could learn the source locations without necessarily visiting the place and possibly memorizing the spatial relations of the source locations in a mental map (Fig. 2B). However, the range of such a mosaic map is limited. For greater distances, Wallraff has proposed an olfactory grid map consisting of the relative proportions of various olfactory or other air-borne gradients that can be extrapolated to unfamiliar areas over hundreds of kilometers (2005). This concept reduces a considerable amount of inherent variability in a volatile grid. On the other hand, it makes experimental verification very difficult because of the multiple atmospheric measurements required to make prediction about success of homing and navigation.

A grid map might also be based on the earth's magnetic field. Theoretically, as long as two magnetic coordinates are not parallel they might be used in a map-sense. However, many uncertainties must be clarified before we can apply a magnetic map theory, e.g. the degree of sensitivity of a bird to magnetic values must be determined, and the angular difference between magnetic isolines and a precise calculation of the geomagnetic values near ground levels must be considered. There is also considerable spatial variation of magnetic information depending on the geographic scale (Phillips, 1996, Walker et al., 1997). Regional gradients in inclination and total intensity could be used in scales above 50-70 km. Local gradients which often differ from the regional gradient in both direction and steepness, may also be used in scales below 5-10 km. However, at intermediate stages, in scales from 10 km to 70 km, local and regional gradients seem to be similar in magnitude, giving higher and lower values in all directions, thus being an unreliable source of information (Phillips, 1996). Figure 3 depicts the homeward orientation of pigeons released at different distances, combining studies from different geographical regions. Schmidt-Koenig (1970) found that there was a drop in the initial orientation of homing pigeons when released at 20 to 60 km distance from the home loft implying that different navigational strategies might be used for short and long-distance homing. Studies on the

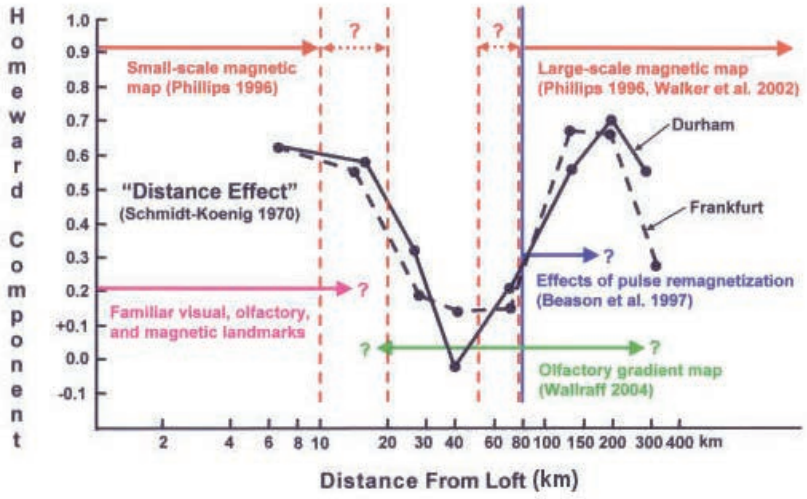

Fig. 3. Effect of distance on the homeward orientation. The solid black line connects data of the homeward orientation of pigeons released at sites around Durham, NC USA. The dashed black line connects data of the homeward orientation of pigeons released at sites around Frankfurt, Germany. Horizontal arrows show predicted range of magnetic gradient maps (orange), olfactory gradient maps (green), familiar landmarks (purple), and range of distances at which pulse remagnetization was found to affect pigeon homing (blue). Vertical lines show boundaries of predicted ranges. Question marks indicate where boundaries are not specified. Courtesy of Prof. J. Phillips [2].

influence of magnetic parameters on orientation are high in number and there are numerous reviews (Wiltschko et al., 1996, Walcott, 2005, Phillips et al., 2006). Overall, results have shown that pigeons appear to sense anomalies, but the effects were quantitatively weak and vary strongly between release sites. Until now, the conclusion has persisted that it is unlikely that navigation is based on a geomagnetic bi-coordinate map alone and that its importance may differ depending on conditions for geomagnetic navigation in regions around the globe (Boström et al., 2012).

Another possible aid for navigation is infrasound. Infrasound waves originating from geomorphological sources might form a grid of gradients (Hagstrum, 2000, 2013). Essentially, Hagstrum's conclusions are based on multiple records made by Keeton and colleagues from releases with pigeons from only one loft, the Cornell loft. The pigeons were always disoriented at Jersey Hill except at one release that was coincident with meteorological records indicating that infrasonic waves were reaching that release site, which was apparently not the case under normal conditions. Pigeons are sensitive to infrasound (Kreithen et al., 1979) but there is no other evidence on the influence of infrasound on navigation and thus, the findings remain scanty.

The role of gravity

The influence of gravity on orientation and the homing process of pigeons has been considered only in a handful of studies. Yeagley, a professor of physics, proposed an organ sensing the shear of the coriolis force during flight which results from the relation between the earth's rotational velocity and motion of a body over the earth (1947). The forces involved are a direct function of the earth's rotational speed, the speed of a body moving over the earth's surface, and the latitude of the moving body. Thus, when the bird is displaced north or south, it will search for the correct correlation of its flight speed with the magnitude of this force. The lines of the coriolis force are coincident with latitude and could form one gradient in a global grid. Yeagley proposed as a second gradient the vertical component of the earth's magnetic field whose isolines intersect with the lines of the coriolis force and therefore would provide a global navigational grid. Despite the experimental evidence for his theory, there is doubt on the accuracy of the proposed grid as a considerable portion of the lines are parallel to each other or tangency occurs and thus cannot pinpoint a unique location.

Larkin and Keeton have investigated the influence of gravitational changes due to the moon's orbit on the initial bearings of homing pigeons (1978). They observed that many pigeons deviated from a direct homeward course in a repeatable fashion and wanted to investigate its causes. They collected data from three different sites during four years and found a monthly oscillation of the mean vanishing bearings; some were from new moon to new moon and some from full moon to full moon. After analysis, they found that the oscillations were almost exactly aligned to the synodic lunar month which is the time when the moon completes its orbit, and that the turning points were the syzygies (new moon and full moon). However, gravity varies along a modified sinusoidal curve whereas the observed oscillations did not and gravity varies twice each month. Nonetheless, Larkin and Keeton found that the homeward component of horizontal acceleration varied statistically with lunar days and its variations resembled how the bird's orientation varied with the lunar days. Despite the fact that they could not demonstrate a direct relationship between the gravitational changes and the mean vanishing bearings of the pigeons, the results suggest this possibility.

Lednor and Walcott were the first to investigate the initial orientation behavior of pigeons released from gravity anomalies. The gravity anomalies were produced by salt domes, which are less dense than the surrounding rock and gave rise to a negative gravity anomaly. Their results showed no affect of the anomaly on the initial orientation of young pigeons. Unfortunately, only pooled results

were given and they did not present any information on the training direction, days of releases nor the distance between the release sites or a gravity anomaly map. This makes interpretation of the results difficult.

Dornfeldt conducted a thorough multivariate analysis of pigeon homing in relation to geomagnetic, gravitational, topographical and meteorological cues (1991). He released pigeons from different magnetic and gravity anomalies and tested if pigeons flew along the geophysical gradients at the release sites. At magnetic anomalies, the pigeons were better oriented than at less irregular fields but at sites of gravity anomalies (15-49 mGal), the pigeons were less homeward oriented than at less anomalous sites (-9-14 mGal). He concluded that the most important factor accounting for poor homing orientation and performance was gravity anomalies.

Kanevskyi and colleagues had a different approach and examined the flight behavior of pigeons flying over a massive tectonic break associated with a gravity anomaly (1984). They observed that the pigeons showed abrupt changes in their flight paths when crossing the anomaly and also showed some telemetrically assessed changes of the EEG. Kanevskyi proposed a new navigational strategy called the “gravity vector” hypothesis (see next paragraph).

A similar concept has been proposed by Köhler (1975). He envisioned that pigeons memorize a horizontal plane (like a round disk) at the home loft and when they are displaced they compare the memorized plane with the visual horizontal plane at the release site and derive an angular difference from the comparison. The angular difference gives the distance to the home site and the touching points of the two planes (one disk is tilted toward the other) the direction. The angular difference is identical to the angular difference of the corresponding plumb lines. With his novel navigational hypothesis he tried to explain the commonly found deviation of pigeons’ vanishing direction from the homeward direction at release sites. If a bird defines the plane from the optic horizontal line, the panorama, then an oblique horizon would give deviating information. However, with increasing distance from the home site, the difference in the planes due to the earth’s curvature predominate the small irregularities of the horizontal planes. Unfortunately, his theory was not further investigated.

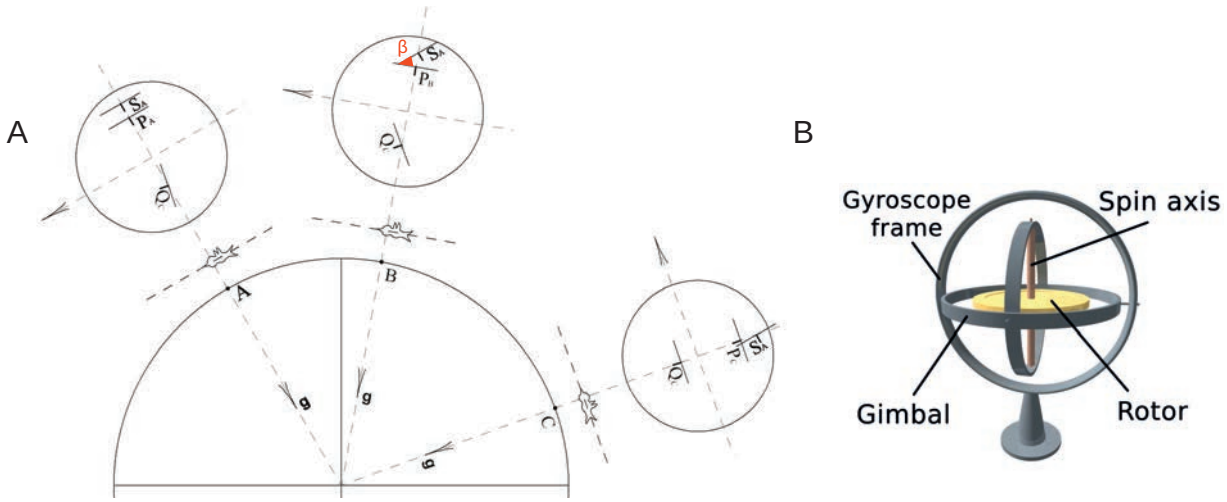

Fig. 4. Illustration of the gravity vector hypothesis. A) A is the memorized home location. P_A is the plane perpendicular to the gravity vector g_A. The plane S_A is perpendicular to the axis of the gyroscope. β_A is the deviation of the two planes, at A, $\beta_A = 0$. After displacement to B: the plane S_A is still perpendicular to vector g_A and the new perceived plane P_B is perpendicular to g_B. The bird can sense the difference of the two planes as β_B. The place C depicts the situation of migrants, where C is the wintering grounds and g_C the genetically memorized gravity vector with its perpendicular plane Q_C. Courtesy of V. Kanevskyi [3]. B) A mechanical gyroscope.The gyroscopic frame holds the rings or gimbals that rotate freely around their axis. The rotor spins always perpendicular to the inner gimbal. From Wikimedia Commons via LucasVB [4].

The gravity vector hypothesis

The gravity vector hypothesis was first formulated by Kanevskyi in 1984 and proposes how animals might find their way home from distant places.

The gravity vector is the sum of acceleration and the centrifugal force of the earth. The direction of a local gravity vector at the surface of the earth is the product of vertical and horizontal forces, and it should always point towards the earth's centre, except in border regions of anomalies with a stronger horizontal component. In other navigation theories, for example those invoking the inclination of the magnetic field changing with latitude, the gravity vector is the ubiquitous reference system for calculating the angle between field lines of gravity and magnetism. For the sensory system of humans, gravity pulls everywhere into the same direction, the so-called subjective vertical (indicated by the direction of a plumb), and there is no way to compare one vertical with another vertical. Kanevskyi's theory avoids this problem by observing the workings of classical mechanical gyroscopes as used in aircrafts and missiles. A mechanical gyroscope uses wheels that are spinning with high speed suspended in so-called gimbals, which permit movement of the axes of the gyroscope (Fig. 4B). Once activated, the spinning wheels maintain the direction of the gravity vector at the starting location regardless of its displacement. In this view, the gyroscope is a mechanical memory of a gravity vector. In theory, the memorized and the actual gravity vector converge in the centre of the earth. Simple

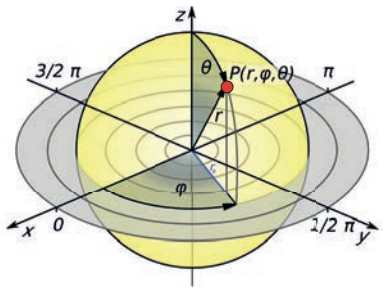

Fig. 5. Schematical view on spherical coordinates. Polar coordinates can be depicted in 2D but to mimic the shape of the earth, we show the scheme of spherical coordinates which are polar coordinates amended with a second coordinate φ. r is the gravity vector, θ the difference to the location at z=0. The red point is defined by the gravity vector, θ and φ (φ=0° for our hypothesis). From Wikimedia Commons via Ichijiku [5].

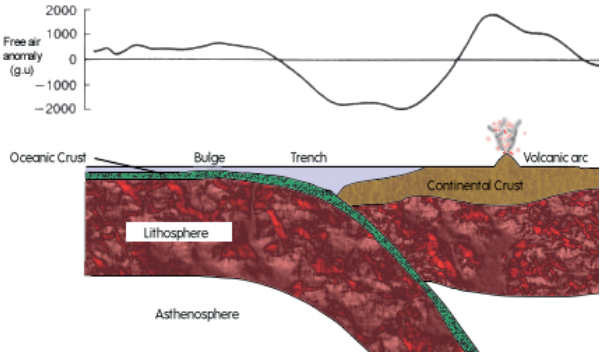

Fig. 6. Example of formation of gravity anomalies. At the subduction zone, the density of mass is low and thus produces a negative anomaly. In the volcanic area, the density of mass is high and thus produces a positive anomaly. Courtesy of Dr. J. Hill [6].

trigonometry permits to compute a projection of two vectors on the surface of the earth. This results in a so-called spherical polar coordinate system, in which the difference between the two points created by intersection of the vectors with the surface of the earth is expressed as direction (azimuth) and distance on the surface of the earth. In contrast to bi-coordinate grid models, the polar coordinate system provided by two gravity vectors does not need a second gradient of different geophysical nature, all information is derived from the comparison of two gravity vectors only (Fig. 5).

Kanevskyi extrapolated this situation to biology by postulating a bio-gyroscope: pigeons (and other birds and long-distance navigating species) undergo imprinting to the local gravity vector, that is, the bird develops a neural representation of the home gravity vector in the first weeks of life. Since the resulting neuronal activity pattern can be maintained independently of the actual sensed gravity direction, a pigeon learns by flying in the loft region that the actually sensed gravity vector feels gradually different the farther from home it is, while memory and actually sensed vector coincide perfectly at the home loft. In doing so, it also learns that the changes in gravity vector experienced by moving homewards are very regular. When the animal is transported to an unknown site, it can calculate its position with respect to home simply by comparing the actual gravity vector sensed with the memorized one (Fig. 4A). Problems in orientation, however, arise when the sensed or memorized gravity vector deviate from the expected directions. This can happen in locations with gravity anomalies.

The earth is not a perfect globe and can be conceived as a geoid (the earth viewed as a hypothetical ellipsoid with the surface represented as a mean sea level). However, there are still slight

deviations in both the magnitude and direction of gravity across the earth's surface. Some deviations are caused by altitude, topography and latitude and are commonly included in computations. Other deviations, called gravity anomalies, are based on uneven distribution of underground masses caused by tectonic breaks where one tectonic plate moves below another, by underground inclusion of denser material containing heavy minerals, or at places where heavier parts of the earth's crust have been removed by volcanic activities or meteor impacts (Fig. 6). In such places, the direction of the gravity vector becomes slightly tilted with respect to its theoretical orientation, because (simplistically expressed) the field lines of gravity are bent towards (or away) from the underground inclusion, depending on the centers of gravity.

Thus, the gravity vector theory predicts that:

(i) pigeons reared within a gravity anomaly and released in a normal gravity area should show deviations in their initial orientation as they miscalculate their position due the relative distortion of the memorized home vector.

(ii) pigeons from lofts in normal gravity conditions and released in gravity anomalies should show deviations in initial orientation as they miscalculate their position due to the distorted vector at the release site.

(iii) pigeons crossing gravity anomalies should show changes in their flight paths.

(iv) pigeons should show better homeward orientation when released from distant release sites as the angular difference increases with distance.

Prediction (iv) is also shared with other navigation theories based on geophysical cues changing constantly with distance (e.g. magnetic inclination angles).

The gravity vector theory as formulated here allows the inclusion of other cues such as geomagnetic and olfactory information depending on species or individual experience. It does not predict the navigational strategy used by the pigeons, which may include extremes such as a pure map-and-compass strategy (the bird defines a flight direction and distance once at the release site) or a simple continuous reduction of gradient differences.

Aims of the thesis

The aim of this thesis was to resolve two important issues in pigeon navigation:

(i) Can pigeons memorize large-scale navigational maps beyond their home range?

(ii) Do gravity anomalies disturb the orientation ability of pigeons, thus providing support for the gravity vector theory?

(i) In a first chapter, we analyzed whether there is a cognitive map sense in pigeons, as opposed to a gradient-reading strategy, which implies that the pigeons return in a robot-like fashion by following geophysical or airborne gradients until they arrive at their home loft. If a pigeon can determine its position and two other distant positions, it has a memory not only of the single positions but their relation to each other, which is the definition of a spatial cognitive map (Tolman, 1948). To test whether pigeons use a cognitive map in an unknown region, we had to train them to a second target other than their home loft, namely a food loft. Pigeons were then released in an unfamiliar area and, depending on feeding motivation, either chose a direction towards the home loft or a direction towards the food loft at the beginning of the flight. GPS-tracking in one experiment showed that they corrected their flight directions even after detours induced by topographical obstacles. Thus, this study provided strong evidence that the pigeons have a cognitive large-scale map, and that they can use a map-and-compass strategy. This study has been accepted for publication (Blaser et al., 2013, J Exp Biol, in press).

(ii) In a second chapter, we tested two specific predictions made by the gravity vector theory. Pigeons were reared on gravity anomalies with gravity gradients perpendicular to each other and released from a gravitationally normal site. The results indicate that the pigeons departed according to the gradients on which they grew up. The second prediction, that pigeons crossing massive gravity anomalies should show deviations in their flight path, was also met. In addition, the data suggested that the birds appeared to be more sensitive and reactive to gravity anomalies than to magnetic anomalies. This study has been submitted for publication (Blaser et al., PLOS ONE, submitted).

(iii) In a third chapter, we tested again the second prediction, that pigeons might change their initial flight course when crossing a gravity anomaly but at this anomaly there were no magnetic disturbances. Furthermore, the gravity anomaly was circular-shaped with normal values in the centre.

Hence, we predicted that pigeons would depart normally from the center of a large gravity anomaly, but might change their flight course after crossing the circular anomaly. In this so far unpublished study we compared the GPS tracks of birds released from within the anomaly with those released from a control site. The birds from within the anomaly were initially less oriented than those of the control site, but corrected their course homewards still within the anomaly. After having crossed the border zone, and encountering a second anomaly in their home direction, they dispersed to the right and to the left and maintained a wrong course over 50 km or more, while the birds from the control site converged much better, except for pigeons flying into gravity anomalies. The results are in line with the observations from the previous study and strengthen thereby the validity of the gravity vector hypothesis. This study is in preparation for submission (Blaser et al., J Exp Biol, in preparation).

Taken together, the thesis shows that the map sense of pigeons is cognitive, it confirms the map-and-compass theory of navigation and shows that an essential part of their navigation system is sensitive to gravity anomalies.

General description of methods

Homing pigeons

Homing pigeons, also named carrier pigeons, are domesticated pigeons of *Columba livia*, the rock pigeon (Levi, 1963). Rock pigeons are native to Europe, North Africa, the Middle East and South Asia and originally live in high places such as cliffs and caves near the sea (Fig. 7). The domestication of the rock pigeon appears to have occurred in the eastern Mediterranean region between 5'000 and 10'000 years ago. The first anecdote of the domestication of pigeons is 4000 years ago when ancient Egyptians reared pigeons for their eggs, their droppings (as fertilizer) and as a food source [7] (Fig. 8). Later, the semi-domesticated pigeons were introduced to Europe by the Romans. The pigeons that we see now in villages and cities have been living with humans hundreds of years, nevertheless, they are not domesticated nor wild pigeons but feral pigeons which means they are descendents from the domesticated rock pigeons. According to the International Code of Zoological Nomenclature, wild, feral and domesticated pigeons have the same name *Columba livia*.

Feral pigeons roost in holes and sheltered ledges under roofs of houses, in barns or churches while the wild pigeons seek shelter in holes in cliffs. *Columba livia* may breed all year long, but mostly stop with the onset of molt end of August. Some might start breeding again in October or November. The females lay a clutch of two eggs and both sexes incubate during 17 days. The youngsters are fully-fledged after about 4 weeks but will still be fed by the parents for another 1-2 weeks. Their natural predators are peregrine falcons and hawks, in urban settlements cats and humans can be a threat.

The homing pigeon is a specific breed, being selected for its homing performance for over hundreds of years. Homing pigeons have served as message bearers from the Assyrian times (1500 BC) until today, the first documented use was by Caesar in the Gallic wars (Levi, 1963). In Switzerland, the army had a homing pigeon branch until 1995. Around 30'00 homing pigeons were available as 'self-reproductive mini aircrafts' [8]. Today, homing pigeons are mostly used as a hobby in racing competitions, either conducted from a release site to the home lofts of the various owners, or with young pigeons brought to one common loft (one-loft races, Fig. 9). A yearly happening is the Sun City

Fig. 7. Rock dove in natural habitat on cliffs Hunstaton, Norfolk, UK. Copyright Andrew Dunn, CC license [9].

Fig. 8. Ancient Egyptian pigeon house 44 AD. Picture taken from the Pigeon Control Resource Centre [10].

Fig. 9. Release of 30'000 racing pigeons from a truck in Ireland. Copyright roscreaonline [11].

Million Dollar Pigeon Race held in South Africa. The owner of the first pigeon wins US$ 125'000. Likewise, winning pigeons are sold to pigeon fanciers for thousands of dollars.

Pigeons have a strong homing drive, are easy to keep in aviaries, usually fly home directly without stopping and set their flight course at the beginning of departure. These characteristics have made the homing pigeon an excellent animal model for investigating experimentally navigation and orientation. However, critics might state that the homing pigeon is first, a domesticated animal and second, it has been selected for specific traits. It seems very unlikely that innate capabilities to navigate are lost in selective breeding or domestication. Clearly, novel navigational strategies cannot suddenly appear in the genus of *Columba* and therefore, what we observe today is what has been preserved. However, there is distinct evidence that use by humans has shaped and selected intraspecific traits important for navigation, which includes physical abilities, motivation, and brain mechanisms important for homing. For one, the homing drive of homing pigeons is stronger than in the rock pigeon (Alleva et al., 1975) and exceeds the one of other well-flying pigeon races. Likewise, street pigeons have the ability of homing but are much more opportunistic in establishing new breeding sites. Homing pigeons differ from non-homing pigeon races in the size of the olfactory bulb (also overdeveloped in long-distance migratory birds such as albatrosses), and the hippocampus (Rehkämper et al., 2008). Navigational capabilities play a minor role in races as the pigeons are usually trained in the same direction and its performance relies more on its physical strength, its motivation and persistence. Discoveries on the navigational abilities of homing pigeons are often regarded as being applicable for birds, mostly migratory birds as well. *Columba livia* does not migrate, but there are closely related species that migrate such as the *Columba palumbus* (Wallraff, 2006) and the extinct passenger pigeon *Columba migratoria* [12]. Nonetheless, there might be differences among pigeons and other bird

species in orientation and navigational strategies, however, with the homing pigeon scientists have collected a solid body of knowledge over the past half a century of extensive research which could not have been achieved with wild birds. As tracking technology advances, very light tracking devices can be mounted on small migratory birds which will open great possibilities to investigate their behavior during migration.

Charles Darwin had examined the differences among pigeons in his manuscript "The variation of animals and plants under domestication" (1868) [13]. His reasoning of choosing the pigeon is as he wrote:

"I have selected this case, because (...) the materials are better than in any other; and one case fully described will in fact illustrate all others."

GPS tracking

In traditional homing pigeon research, only the initial orientation observed with binoculars, and the homing performance, which is the duration of the pigeon's flight over the distance, could be analyzed. There was absolutely no information on how the birds behaved during flight. Some researchers followed the pigeons by helicopter (Wagner, 1970) while others used radio telemetry and airplanes (Walcott, 1977). However, helicopters and airplanes are very expensive, and the tracks imprecise whereas radio telemetry is limited in range.

We applied the tracking method of a satellite-based global positioning system (GPS). GPS loggers are small devices that collect positional information from a minimum of three satellites, which it connects to through an antenna (Fig. 10). Once a connection is established, the device stores the information in form of longitude and latitude for each position per second. We had state-of-the-art GPS loggers from Technosmart, GiPSy-2, which were on average 12 g and 3.5x 2.8 cm large (with battery). It had an on-board memory of 8 MB and a storage capacity of 800'000 positions. We used light-weight lithium batteries that could run for 4 to 6 hours if the GPS had an operating mode of 1 Hz (1 fix/s). The accuracy of position increases with the number of satellites and on the operating mode. For example, with an interval of 1 Hz, 95% of the fixes recorded are in a radius of 4.2 m (50%

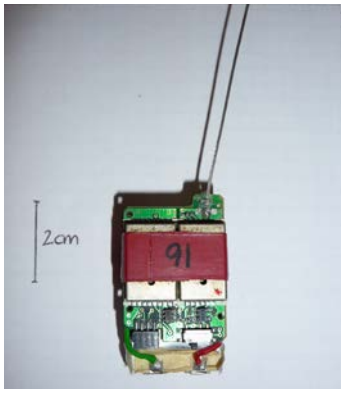

Fig. 10. GPS device with antenna.

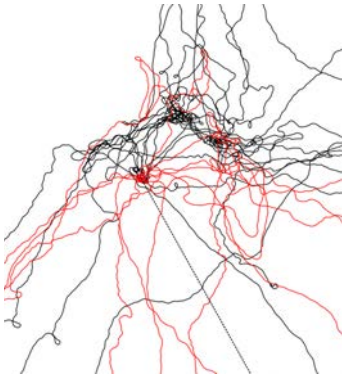

Fig. 11. Flight tracks visualized in QGIS. Red and black lines are flight tracks, the dotted line is the homeward direction.

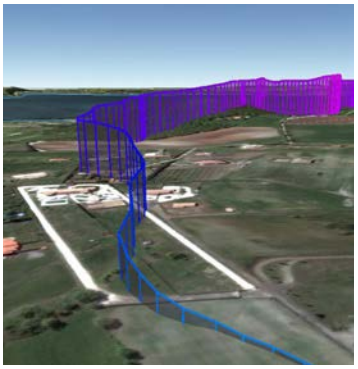

Fig. 12. Flight track of pigeon is connected through lines to the ground which indicate the elevation. Color coding shows flight speed.

within 2.5 m). Along with the position, the time, the date, the speed, the altitude and other parameters are saved. After usage, I connected the device to a computer and downloaded the data with the GiPSy software. The flight tracks can be plotted on a virtual map and various flight parameters can be analyzed (Fig. 11, 12).

Geophysical maps

Gravity anomalies have been subject to careful mapping by geophysicists and geologists, because they provide information for mining of minerals, oil and gas. The vertical component is generally assessed by means of accelerometers, while the horizontal components can be assessed by so-called gradiometric procedures, nowadays also by computation. Historically, the first measurement of the horizontal component was done by Loràn d Eötvös who invented as torsion balance (Eötvös pendulum) for identification of underground masses exerting a horizontal force (the gravity gradient “E”, named after him) [14]. This horizontal component is much stronger in the border zone of a gravity anomaly where the vertical component changes rapidly, while the center of a gravity anomaly may show higher or lower vertical acceleration, but generally its horizontal component does not differ much from the ideal geoid. Thus, modern geophysical mapping provides areas with strong gravity gradients indicating the presence of a slightly tilted gravity vector. Such bending of the gravity vector is important for geologists seeking oil or mineral resources, but it also has the potential to influence any gyroscope-based navigation mechanism. Therefore, precise information about gravity anomalies of sufficient magnitude to change the course of missiles has been classified in many countries, and

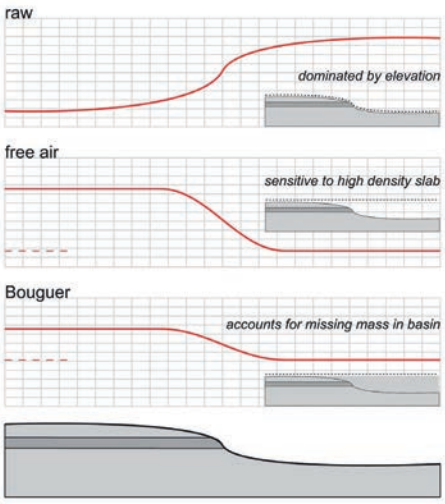

Fig. 13 Gravity profiles. The raw gravity profile is dominated by elevation. The free air anomaly is caused by changes in mass after correction of latitude and altitude. The Bouguer anomaly corrects also for topography. Courtesy of Prof. M. Dumberry [15].

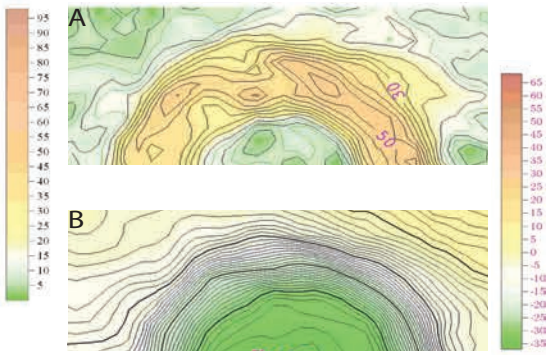

Fig. 14. Gravity anomaly maps.A) Horizontal gravity gradient map, highest values mark locations with steepest gradient of gravimetric values in border zones of gravity anomalies. The scale on the left depicts E (E = Eötvös). B) Gravimetric or Bouguer anomaly, the change of the gravity intensity (ΔG_B – Bouguer). The scale on the right depicts ΔmGal.

became available in many countries only recently, in the Ukraine in 2011. However, these maps are essential for testing the gravity theory.

We show two types of gravity anomaly maps, the gravity intensity and the horizontal gradient of gravity. The gravity intensity anomaly map is a Bouguer anomaly map. The Bouguer calculation corrects for latitude, pull of rock bodies in the surrounding area and for surface terrain and thus is also called the Bouguer anomaly map, expressed in ΔgB (indicated as Δ mGal in Figures and simply as mGal in the text, Fig. 13). In Ukraine, deviating terrain were the slopes of the rivers and corrections usually did not exceed 1 mGal. The Bouguer anomaly map shows the gravity intensity in mGal with contour interval levels at 5 mGal. Gal is a unit of acceleration, 1 mGal = 10 - 6 g, 1 Gal = 1 cm/s² = 0.01 m/s². The gravity acceleration increases towards the poles (26 mGal/100 km) and decreases with altitude (30 mGal/100 m). In comparison, local anomalies can vary up to 200 mGal while variations due to the lunar cycle are around 0.3 mGal.

The Bouguer anomaly map is a traditional way of showing gravity anomalies (Fig. 14B) and it is comparable to the horizontal gradient map. The Bouguer anomaly map is also easier to read and intuitively, one can imagine the gravity vector to be vertical where the contour lines are far apart whereas when the contour lines lie close together a change in the horizontal component is apparent and sometimes even its direction. Therefore, we have also included Bouguer anomaly maps despite the fact that intensity values are of minor interest for the gravity vector hypothesis.

The second type of gravity anomaly maps shows the horizontal gravity gradient of the earth, that

is, the horizontal change in the gravitational acceleration vector from one point on the Earth's surface to another and is customarily measured in units of Eötvös (E) (Fig. 14A). One E is 0.1 mGal/km. The horizontal gravity gradients were calculated by using the Bouguer anomaly data: gravity difference in neighboring points, divided by the distance between these points. For both anomaly areas in the two studies, the maximum change is 55 E.

The gravity maps include different levels of resolution. The high-resolution maps (scale 1:10'000) are largely based on a grid of 100 x 100 m with an accuracy of 0.1 mGal. The other maps (scale 1:200'000) were composed from terrestrial surveys including cell grids of 250 x 250 m, 250 x 500 m, and 500 x 500 m. The Bandurove gravity anomaly in our first project in Zavallia, showed an average amplitude, which is the difference between the value at the center of the anomaly and the mean anomaly in the environmental field, of 30 mGal. The largest amplitude from the north was 40 mGal.

Some parts of the magnetic maps were made in an aeromagnetic survey with a scale 1:200 000 (2 km flying height, the distance between flight lines 2 km) in the years 1951-1959. Other parts were composed from aerial (50 m altitude) and terrestrial surveys (observation lines of 100 or 250 m distance, respectively). The contour interval levels are 50 nT (nanoTesla).

The Bandurove gravity anomaly in the test area of our first project in Zavallia showed also magnetic variation. The release site Pologi showed a magnetic intensity of 329 nT, the homeloft area in the village Zavallia 384 nT and the homeloft area in the village Savran 206 nT. The difference from the release site to a point 2 km in the homeward direction was 16nT. In general, peaks of magnetic variation were dispersed in the test area and did not overlap with the main gravity anomalous area 15 km north of the home loft Zavallia. In our second project in Ukraine, there was no overlap of magnetic variation with gravity variation in the Boltischka region.

Study sites

First project in Italy

The primary reason why the pigeon studies were conducted in Italy is that the high density of (legally protected) raptor birds made extensive pigeon studies in Switzerland more and more difficult. The second reason was that the Italian coast contains geomagnetic anomalies below the sea level. Thus, the Institute of Anatomy moved several mobile pigeon lofts to Italy and established a field station for

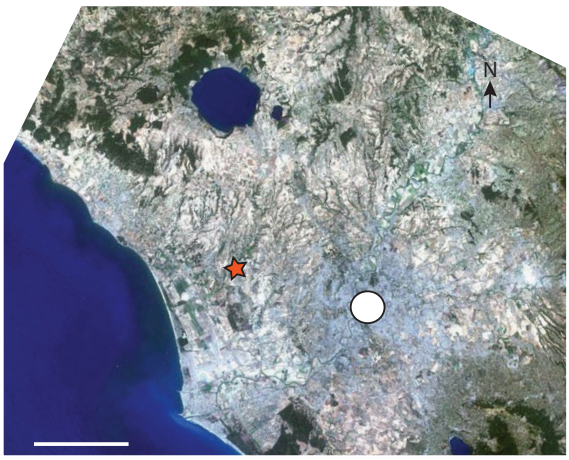

Fig. 15. Satellite image of Lazio, Italy. The red star indicates the position of the pigeon loft in Testa di Lepre, close to Rome which is indicated by the white circle. The lake is lake Bracciano. The scale bar denotes 10 km. Data available from the U.S. Geological Survey [16].

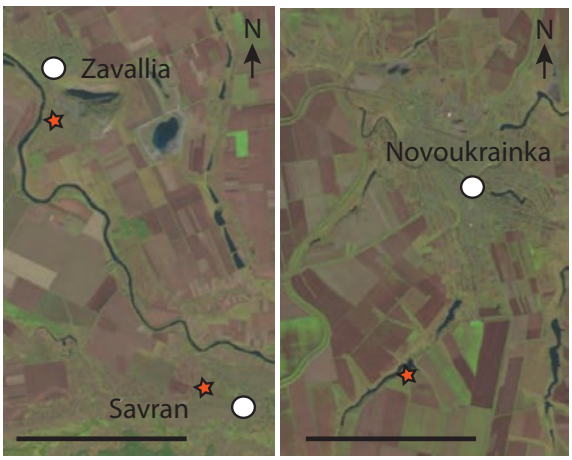

Fig. 16. Satellite image of Ukraine. The red star indicates the position of the pigeon lofts in the respective towns, Zavallia, Savran, Novoukrainka, indicated with a white circle. The scale bar denotes 5 km. Data available from the U.S. Geological Survey [17].

pigeon research at Testa die Lepre (Fig. 15, N 41°55', E 12°16', 35 m a.s.l.), northwest of Rome, using it for a variety of studies (Lipp et al., 2004, Vyssotski et al., 2009, Dell'Ariccia et al., 2008, 2009a, 2009b). The pigeon loft had a special location, being situated in a shallow creek (Arrone valley), so that the pigeons could not see it from distance.

Projects in Ukraine

We established collaboration with V. Kanevskyi, Director of the High-Technologies Institute in Kiev, to investigate gravity anomalies. Ukraine is an ideal country for studying geophysical anomalies without topographic features as it is completely flat apart from the Carpathian Mountains in the west, and the Crimean Mountains on the Crimea peninsula. In addition, it offers a similar climate as Italy, with almost no rain during spring but hotter summers. The most important advantage was the flat topography and the occurrence of strong gravity anomalies. In Switzerland, gravity anomalies also exist but they usually correlate with topography, e.g. mountains. We transported former Swiss army lofts to Zavallia (N 48°11', E 30°0'), Savran (N 48°8', E 30°4') and Novoukrainka (N 48°16', E 31°30'), villages in the southeastern Ukraine (Fig. 16).

Chapter 1

Testing cognitive navigation in unknown territories: homing pigeons choose different targets

Authors

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Summary

Homing pigeons (*Columba livia*) are believed to adopt a map-and-compass strategy to find their way home. Surprisingly, to date a clear demonstration of the use of a cognitive map in free-flight experiments is missing. In this study, we investigated whether homing pigeons use a mental map in which - at an unknown release site - their own position, the home loft and a food loft are represented simultaneously. In order to test this, homing pigeons were trained to fly to a 25-30 km distant food loft. A total of 131 hungry and satiated pigeons were then released from an unfamiliar site equidistant from the food loft and the home loft. Their vanishing bearings and homing times were assessed conventionally at four sites, and from one release site their flight tracks were also assessed by means of GPS loggers. The vanishing bearings of fed and hungry birds differed significantly at all release sites and a highly significant portion of hungry birds flew to the food loft, while the fed birds headed home. The GPS experiment revealed a number of pigeons flying very precisely to the food loft, others correcting their flight direction after topography-induced detours. This implies that the pigeons knew their geographical position in relation to the targets, and chose a flight direction according to their locally manipulated needs – clearly the essence of a cognitive navigational map.

Introduction

True large-scale navigation, as observed in migratory birds and pigeons, requires goal-oriented behavior in unknown territories. Until now, the map-and-compass strategy, as formulated by Kramer (1953), has been widely accepted. It proposes a position-determination mechanism as primary step, after which a compass direction to a target is calculated. The compass direction may be updated by position fixes periodically, thus enabling correction of the flight course and detours. Compass mechanisms used for maintaining a target course include celestial cues (azimuth of the sun, stellar constellations), geophysical cues and visual topographic features. So far, most research has been carried out to clarify the nature of the compass mechanisms (Schmidt-Koenig, 1960; Able, 1994; Muheim et al., 2002; Budzynski et al., 2002; Wiltschko and Wiltschko, 2010). On the other hand, the investigation of the map step has remained controversial. Models proposed include olfactory-based position finding (Papi et al., 1973; Wallraff, 2005) and theories invoking bi-coordinate magnetic grids or other geophysical cues (Gould, 1998; Walker et al., 2002).

A less obvious but challenging problem remains as to whether or not position-determination during the map step is cognitive (Bennett, 1996; Cruse and Wehner, 2011). Traditionally, a cognitive map is referred to a mental representation of spatial relations of objects (Tolman, 1948). In terms of large-scale navigation, do the birds really "know" where they are and do they have a set of mental spatial coordinates enabling them to choose different courses? Until now, the use of a navigational map has been investigated in either laboratory settings (Cheng, 1994; Kamil and Cheng, 2001; Blaisdell and Cook, 2005; Gibson et al., 2012) or in the natural environment of familiar areas in pigeon homing (Holland, 2003; Bingman et al., 2005a; Gagliardo et al., 2009). Vanishing bearings of pigeons released in-between a former and a new loft provided some evidence for the use of cognitive navigational mapping in homing pigeons (Baldaccini, 1976). In addition, most pigeon breeders have experienced the return of pigeons after long periods of absence (either through losses in races or by sales to colleagues), suggesting that pigeons can memorize different loft positions. However, a systematic and experimental study with pigeons released from completely unknown regions is missing.

Displacement experiments with migratory birds have provided evidence of a large-scale navigational map (Akesson et al., 2005; Thorup et al, 2007; Chernetsov et al., 2008; Holland et al., 2009), as did tracking studies of bartailed godwits crossing the pacific along different routes (Gill et al., 2009). However, until now, migratory birds were never manipulated locally for setting different compass directions to elucidate whether they are able to choose between memorized targets. Therefore, displacement studies cannot illustrate the use of a cognitive map. A cognitive map requires a minimum of two concurrently memorized sets of target coordinates, and, at an unknown release site, a computation of the pigeon's position in relation to the targets to choose a compass direction. Conceptually, it has not been ruled out that pigeons orient according to a navigational principle using only one mental set of coordinates: the home loft. This would allow the birds to navigate home using simpler strategies, e.g. near-automated following of various gradient differences (olfactory, magnetic) until they reach home (called "loftocentric" strategy here). Obviously, such a strategy would not correspond to a cognitive map-and-compass strategy.

To test whether pigeons use a "loftocentric" or a true

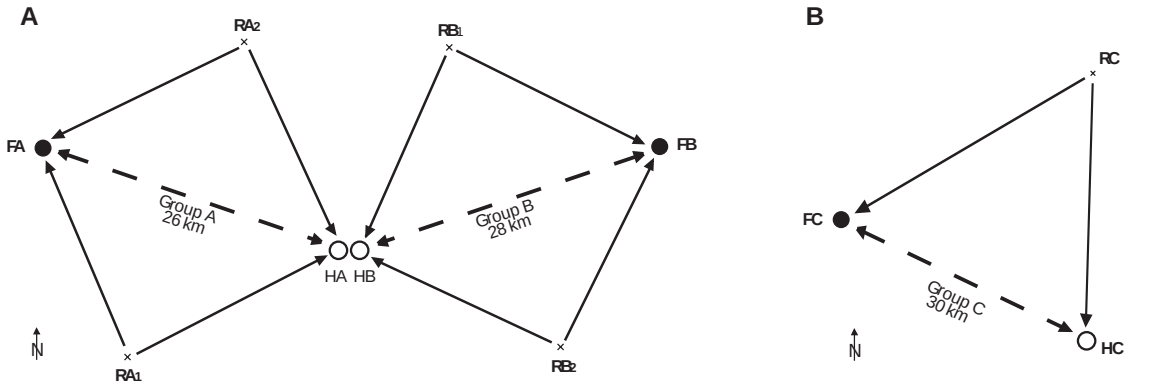

Fig. 1. Scheme of the experimental design of pigeon trainings and releases in the vanishing bearing experiments (A) and in the GPS experiment (B). (A) In Switzerland, group A was trained along the beeline from the food loft FA to the home loft HA whereas group B was trained along the beeline from the food loft FB to the home loft HB, indicated with dashed lines. Release sites for group A are indicated with RA_1 (distance to FA 25.5 km, to HA 26 km) and RA_2 (distance to FA 21.5 km, to HA 20.5 km) and for group B with RB_1 (distance to FB 23 km, to HB 23.5 km) and RB_2 (distance to FB 25 km, to HB 28 km). (B) In Italy, group C was trained along the beeline from the food loft FC to the home loft HC. The release site is indicated with RC (distance to FC 31 km, to HC 28 km).

cognitive map-and-compass strategy, one faces the problem that displaced pigeons usually have only one imprinted and ecologically relevant target, the home loft. To set two ecologically relevant goals for the pigeons, we trained homing pigeons to obtain food at a distant loft, flying to the food loft and back to their home loft repeatedly, thus the birds developed a stereotyped corridor path along familiar landmarks. A group of hungry birds and a group of satiated birds (fed at the release site) were then released at unfamiliar places equidistant to both the food and the home loft. If the "loftocentric" strategy would apply, the hungry birds would need to fly home first and reach the food loft by following familiar landmarks. In this case, there would be no difference in vanishing bearings and significantly longer flight times for the hungry birds to reach the food loft than for the satiated birds to fly to the home loft. In case of a cognitive map-and-compass navigation, we would expect significant differences of initial bearings and equal flight times to the respective targets. In addition, when tracking pigeons by means of GPS loggers, we would expect the direction of the flight paths to approximate the target direction. In case of a "loftocentric" strategy, the GPS tracks of hungry birds should not show reorientation toward the target loft before reaching the familiar loft area.

Materials and methods

Vanishing bearing experiments

Young pigeons living in mobile lofts of the Swiss army were transferred from the vicinity of Berne across 150 km to Kirchberg (N 47°25', E 9°1', 695 m a.s.l.), in eastern Switzerland, where none of the pigeons had been before. There, they were placed again in the same mobile lofts. All of the pigeons were one or two years old and had moderate experience (10 to 15 releases from up to 50 km) at their previous home site. In September 1990, they were accustomed to the new location at Kirchberg during 4 weeks according to standard procedures of the Swiss army and also to a feeding schedule of 48 h intervals to increase feeding motivation. Afterward, the pigeons were trained in two groups: group A from home loft HA learnt to feed at food loft FA 26 km westwards (N 47°32', E 8°44', 485 m a.s.l.), while group B from home loft HB had to fly 28 km eastwards to food loft FB (N 47°28', E 9°22', 595 m a.s.l.) (Fig. 1). First, the pigeons were transported to their food lofts by car every second day and were allowed to feed in the food loft. After feeding, they were transported back. Meanwhile, the pigeons were trained from increasing distances to return home from sites on the beeline to the food loft. Such stepwise training was required since the birds lived at an unfamiliar site. After successful completion of the whole journey back to the home loft, the pigeons

were trained to fly into the food loft. They flew first from the vicinity of the food loft; then, with increasing distances, the pigeons managed to fly from the home loft to the food loft, feed there and then return back home. The experimental release sites were chosen to be equidistant from the home and the food loft in an unfamiliar terrain (22 to 26 km distance to home or food lofts, Fig. 1). Thus, group A (28 pigeons) was released from site RA_1 (Mönchaltdorf, N 47°19', E 8°42', 440 m a.s.l.) on a sunny day and with no wind. Two days later, the same group (25 pigeons) was released from a new site, RA_2 (Müllheim, N 47°36', E 9°0', 410 m a.s.l.), on a cloudy day, but with visible sun and a northwesterly wind of about 30 km/h. Group B (28 pigeons) was released from site RB_1 (Ellighausen, N 47°37', E 9°8', 520 m a.s.l.) on a sunny day, partially clouded, with moderate westwind (5-10 km/h). Five days later, group B (27 pigeons) was released again but now from site RB_2 (Schwägalp, N 47°15', E 9°18', 1270 m a.s.l.) on a cloudy day with the sun barely visible and a cool west wind. For all releases, pigeons were transported early in the morning to the release sites and spent one hour in crates from which they could see and smell the surroundings. Prior to departure, half of the pigeons were randomly selected and were fed at the release site, while the other half remained hungry. The pigeons were released pairwise, alternating pairs of hungry pigeons with pairs of fed pigeons, in intervals of 5 min. Pairwise releasing was done to suppress the tendency of the birds to remain in the vicinity of the release site until the release of a companion. For statistics, each pair of pigeons was considered as one data point. Pigeons were not tossed but were allowed to depart from a start box in which they were placed a few minutes before release. This allowed for assessing the departure motivation of the birds.

In order to control for release site effects on the vanishing bearings, and in particular for the possible effect of repeated training from the same direction (Dell'Ariccia et al., 2009a), we released also control pigeons for each experimental group and on the same days. The control pigeons were not trained in the training directions of the experimental pigeons, thus were not influenced by the same training effect as the experimental groups. However, the control pigeons were released from the experimental sites twice for training. The control pigeons were neither hungry nor fed and flew only to their home lofts located in the vicinity of the targets of the experimental birds.

The vanishing bearings were determined by two independent observers with 8x30 binoculars, averaged and rounded to the next 5 degrees. The homing times were recorded from an observer at the home loft. Thus, the mean speed (beeline distance between release site and target/ flight time) was calculated as an indicator of homing performance (hp). The homing performance was compared between groups with the Mann-Whitney U-test (Siegel and Castellan, 1956). The distributions of vanishing bearings were tested for uniformity using the Rayleigh test (Batschelet, 1981). The Watson U2-test was used to show any difference between the groups and the Watson-Williams F-test to depict a difference in the mean vanishing bearings. The mean vanishing vector was computed with the statistical software Oriana (Kovach Computing Services). The mean vanishing vector shows the mean direction of the pigeons' vanishing bearings and with its length (variable between 0 and 1) a reciprocal measure of angular dispersion (Batschelet, 1981). In addition, the homeward component (hc) of the mean vanishing vectors was calculated. The homeward component is the rectangular projection of the mean vanishing vector onto the axis pointing toward home and shows how homeward orientated the group of pigeons was. The number of pigeons choosing either the food or the home loft as their target was analyzed for significance with the Fisher's exact probability test.

GPS experiment

Pigeons were kept in a former Swiss army mobile loft in Testa di Lepre (N 41°55', E 12°16', 35 m a.s.l.), north-west of Rome. The pigeons will be referred to as group C. The food loft FC, also a Swiss army mobile loft and thus familiar to the pigeons, was placed in Santa Severa (N 42°2', E 11°58', 43 m a.s.l.), 30 km north-west of the home loft HC. The pigeons were mixed in gender, age and experience (1 to 5 years old, average 2 years old). Since the beginning of the training, pigeons were fed only every second day and only in the food loft to increase feeding motivation. During six days, the pigeons were brought by car to the food loft, were fed there and then they flew back home in flock. Afterward, the pigeons were released in the vicinity of the food loft to let them fly

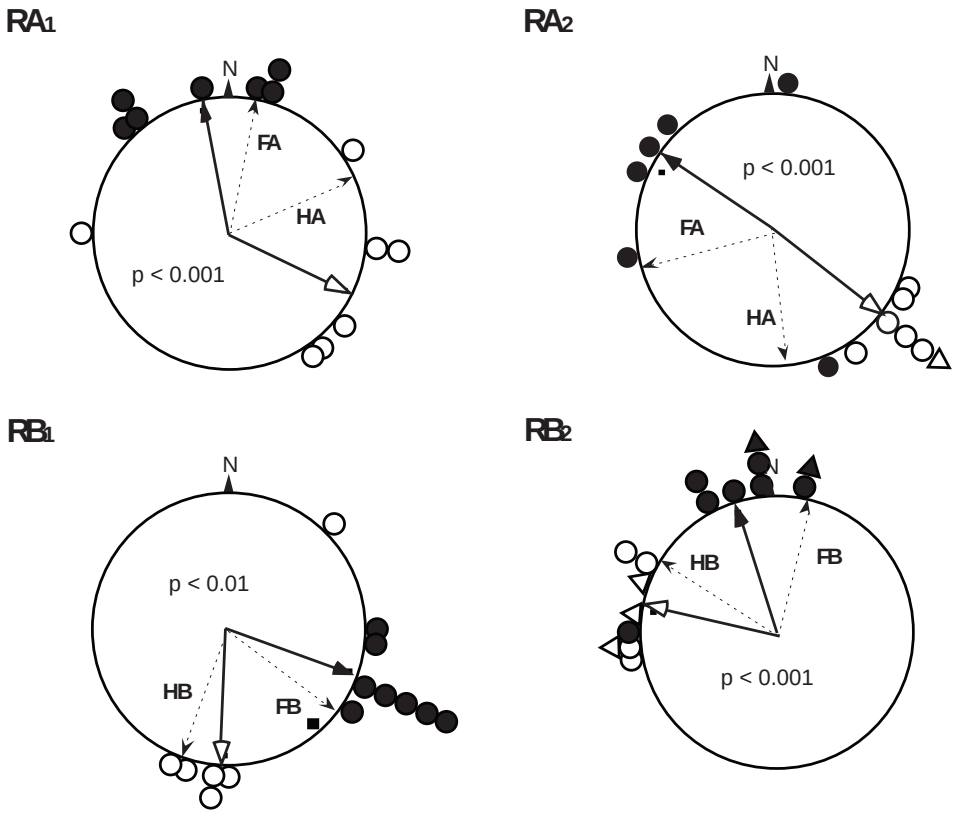

Fig. 2. The vanishing bearing experiments. The black circles refer to the hungry pigeons whereas the white circles refer to the fed pigeons. Circles represent pairs of pigeons, triangles single pigeons. The bold arrows show the mean vanishing bearings of the hungry pigeons with a black arrow head and of the fed pigeons with a white arrow head. The dotted arrows show the home loft direction (HA, HB) and the food loft direction (FA, FB). All values are summarized in Table 1. The difference between the hungry and the fed pigeons for each release was calculated with the Watson-Williams-F-Test for significance (see p-values within the circles). RA1, release site Mönchaltdorf, with 14 pigeons in each group. RA2, release site Müllheim, with 13 fed and 12 hungry pigeons. RB1, release site Ellighausen, with 12 fed and 16 hungry pigeons. RB2, release site Schwägalp, with 11 fed and 16 hungry pigeons.

into the food loft, feed there and then fly back home. The pigeons were released with increasing distances from the food loft near the beeline "food loft-home loft". One month before the experiment, pigeons were equipped with a PVC imitation of a miniature GPS logger to accustom them to the weight and size of the GPS logger (GiPSy2, Technosmart). The PVC dummies were fixated with adhesive tissue (Velcro tapes), glued on shortened feathers on the back of the birds. The pigeons carried the dummies throughout the training period. At the end of the training phase, the pigeons were equipped with GPS loggers to record their training flights (Fig. 5). The release site RC for the experiment (Bracciano, N 42°10', E 12°17', 325 m a.s.l.) was in northeasterly direction from the home loft, equidistant to the home (28 km) and the food loft (31 km) (Fig. 1). None of the pigeons had ever been in that area before. On the day of the experiment, in July 2009, 23 pigeons were transported by car early in the morning to the release site. The weather was good, with no clouds and no wind, but with a slight haziness reducing long-distance visibility. There, the pigeons were kept in crates with visual and olfactory access to the environment for one hour to adapt to the site and to increase motivation to home (Dell'Ariccia et al., 2009b). Then, half of the pigeons were chosen randomly, were put into a separate box and fed ad libitum. The other half remained hungry. The pigeons were then released in pairs in separate starting crates, alternating two hungry and two fed pigeons, at 5-minute intervals between pairs. Beforehand, the PVC dummies were replaced by GPS loggers recording one position fix every second, with an accuracy of about 4 m in 95% of the locations. The data were afterward downloaded from the device to a computer using GiPSy2 software (Technosmart). All files were then imported into the freeware Wintrack (Wolfer et al., 2001) for analysis. We concentrated on calculating vanishing parameters at 2 km from the release site, a choice in accordance with previous literature (Wallraff, 2005). The vanishing times and the lengths of the vanishing flight tracks were extracted from

Table 1. Vanishing bearing parameters and homing performance of all releases in Switzerland

Group	R	N	T	n	L	δ	s	α	r	hc	t	hp
Group A	RA_1	14 f	Home	5 f	8 f	64	7	116	0.60$^{n.s.}$	0.37	4	33
		14 h	Food	13 h	0 h	5	7	347	0.90***	0.81	9	29$^{n.s.}$
	RA_2	13 f	Home	12 f	1 f	177	7	128	0.99***	0.65	9	50
		12 h	Food	10 h	2 h	253	6	297	0.56$^{n.s.}$	0.40	7	33$^{n.s.}$
Group B	RB_1	12 f	Home	9 f	3 f	202	6	183	0.69*	0.65	7	30
		16 h	Food	16 h	0 h	132	8	109	0.98**	0.91	10	45*
	RB_2	11 f	Home	9 f	0 f	318	7	279	0.96***	0.74	5	49
		16 h	Food	15 h	1 h	12	9	344	0.89***	0.77	9	43$^{n.s.}$

Group A pigeons were released from sites RA1 and RA2, while group B pigeons from sites RB1 and RB2. N depicts the numbers of fed (f) and hungry (h) pigeons before release. T is the expected target loft for released pigeons. n is the number of either fed or hungry pigeons that arrived at the target loft. L is the number of lost pigeons. δ [°] is the direction to the target clockwise from north. s is the sample size (pigeons) used for vanishing bearing analysis. α [°] is the mean vanishing bearing of the respective fed or hungry sub-group. r is the mean vanishing vector and hc is the homeward component. t is the sample size (arrived pigeons) used for the homing performance analysis and hp [km/h] is the homing performance (beeline distance/flight time). If t is larger than s, pairs of pigeons separated during the flight. The asterisks refer to the significance levels (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$, n.s. not significant) of the Rayleigh test (r column) and the Mann-Whitney U-test (hp column). These levels are depicted in the hp column in the second line of each group to show the difference within the group.

the data with Wintrack whereas the mean vanishing vector was computed with the stat software Oriana (Kovach Computing Services). In addition, the homeward component (which is the projection of the mean vanishing vector onto the homeward direction) was calculated and is considered as the target-oriented component for both pigeon groups. Other flight parameters were analyzed to show any difference in the homing behavior of both groups: path efficiency (path ef = beeline distance between release site and target/ track length, in %), homing efficiency (hom ef = % of path with homeward component >75%), path linearity (path lin = beeline/ track length in 32 s steps, in %), actual flight speed (speed = GPS ground speed, in km/h) and homing performance (hp = beeline distance between release site and target/ duration of the flight, in km/h); the latter was calculated to compare with the hp of the pigeons in the Swiss experiment. The path linearity is a measure of straightness of the pigeon's track independent of the home direction; the beeline and the track length between two points, 32 s apart, were calculated for the whole track. These parameters were tested for any difference between the two groups with the Mann-Whitney U-test. The vanishing angles were tested for uniformity using the Rayleigh test and the Watson U2-test was used to show any difference between the groups. A difference in the mean vanishing vector of the two groups was analyzed with the Watson-Williams-F-test. The number of pigeons choosing either the food or the home loft as their target was analyzed for significance with the Fisher's exact probability test. On a different day, a control group of pigeons was released at the same site with no treatment (hungry nor fed) to fly home to the same home loft, but there was no control release conducted as a comparison to the behavior of the hungry pigeons flying to the food loft since there was no pigeon loft there. Again, each pair was counted as one data point for all statistical analyses.

Results

In all experiments, hungry pigeons chose significantly the feeding site as their flight target whereas fed pigeons chose significantly the home loft as their flight target (Fisher's exact probability test, combining numbers of all releases: $p<0.001$; for each release: $p<0.05$). Overall, 65 out of 69 released hungry pigeons arrived at the food loft and only one at the home loft. And 47 out of 62 released fed pigeons arrived at the home loft and 3 at the food loft. Only 3 hungry and 12 fed pigeons were lost.

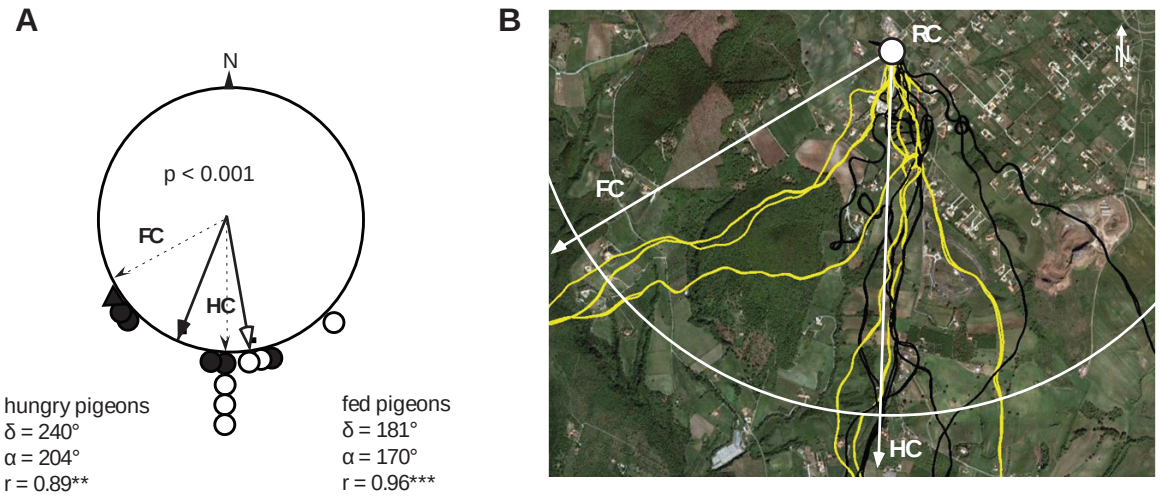

Fig. 3. (A) The vanishing bearings of the pigeons in the GPS experiment. The black circles refer to hungry pigeons (n = 11) whereas the white circles refer to fed pigeons (n = 12). Circles represent pairs of pigeons, triangles single pigeons. The bold arrows show the mean vanishing bearings of the hungry pigeons with a black arrow head and of the fed pigeons with a white arrow head. The dotted arrow shows the home loft direction (HC) and the food loft direction (FC). δ is the loft direction, a is the mean vanishing bearing and r is the mean vanishing vector with significance values (** = p<0.01, *** = p<0.001) of the Rayleigh test. The difference between the hungry and the fed pigeons was calculated with the Watson-Williams-F-Test for significance (see p-value within the circle). (B) Initial GPS flight tracks from RC. The tracks of the hungry pigeons are in yellow and the tracks of the fed pigeons are in black. The white arrows show the directions from the release site (RC) to the home loft (HC) and to the food loft (FC). The diameter of the circle is 2 km.

Table 2. GPS vanishing and homing parameters of the release in Italy

Group	R	N	T	n	s	hc	vt	vp	t	hp	path ef	hom ef	path lin	speed
Group C	RC	12 f	Home	12 f	6	0.94	2.6	2.6	6	50	73.8	75.6	94.9	68
		11 h	Food	11 h	6	0.72	2.1$^{n.s.}$	2.3$^{n.s.}$	7	54$^{n.s.}$	76.7$^{n.s.}$	67.4$^{n.s.}$	96.2$^{n.s.}$	71$^{n.s.}$

Group C pigeons were released from site RC. N depicts the number of fed (f) and hungry (h) pigeons before release. T is the expected target loft for released pigeons. n is the number of either fed or hungry pigeons that arrived at the target loft. s is the sample size (pigeons) used for vanishing bearing analysis. hc is the homeward component. vt is the vanishing time [min] and vp the vanishing track lenght [km] until the bird was 2 km distant from the release site. t is the sample size (pigeons) used for homing analysis. If t is larger than s, pairs of pigeons separated during flight. hp [km/h] is the homing performance, path ef [%] is the path efficiency, hom ef [%] is the homing efficiency and path lin [%] the path linearity. speed [km/h] is the actual speed recorded by the GPS device. The Mann-Whitney U-Test tested any difference within the groups, depicted in the second line as n.s. = not significant.

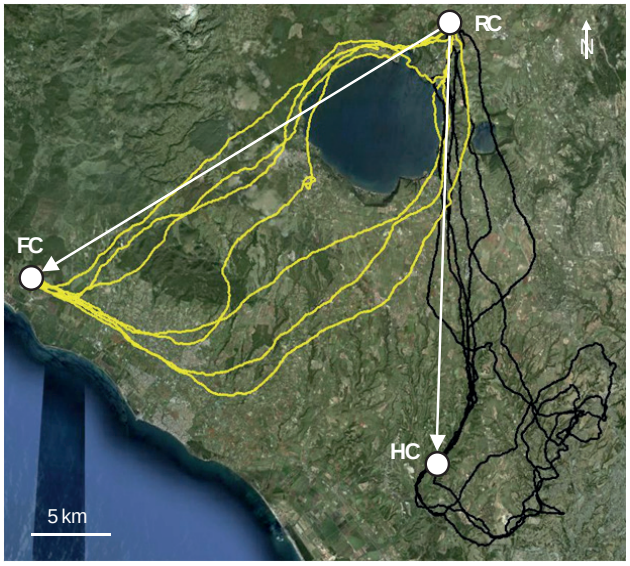

Fig. 4. Flight tracks of all hungry and fed pigeons in the GPS experiment. The yellow tracks show 4 hungry pairs and 3 single pigeons. The black tracks show 6 fed pairs. RC is the release site, FC the food loft and HC the home loft. The big lake is lake Bracciano, the small lake easterly is lake Martignano. The distance from the release site to the food loft and home loft is 31 km and 28 km, respectively. The direction from RC to FC is 240°, from RC to HC 181°.

Fig. 5. Flight tracks of 11 pigeons flying in the training corridor. FC refers to the food loft and HC to the home loft. The red circle is the training release site. The pigeons were released from the training site, then they flew first to the food loft and after resting there for one to two hours they were released to fly back home.

Vanishing bearing experiments

A summary of all vanishing parameters and homing performances of pigeons that participated in the four releases in Switzerland is shown in Table 1. The vanishing bearings of the hungry and fed pigeons in each release were significantly different (Fig. 2). Six out of 8 released groups of experimental pigeons showed also a significant orientation (Rayleigh test, Table 1, parameter r). One exception was the release at site RA1 (Mönchaltdorf), where the fed pigeons showed a poor homing success (8 out of 14 were lost) and a scattered initial orientation due to one pair that headed in a direction away from the home loft for unknown reasons and three pairs that headed for the training direction, thus impairing the directionality scores. The control birds supposed to fly to the same target showed largely similar bearings but without outliers (Fig. 6). Northeast of the release site is a mountain chain (1000-1200 m a.s.l.) lying between release site and target with a mountain slope starting only a few km away from the release site. Another exception was the release at site RA2 (Müllheim), where the vanishing bearings of the hungry pigeons were not significantly different from random, which was mainly caused by one pair flying in the opposite direction. Also four control pairs of pigeons scattered in the opposite direction. The hungry pigeons were also deviating from the direction to the food loft aligning to the training direction but the control pigeons showed a similar pattern. At the same site, the fed pigeons choose a direction that coincided with the training direction, while the control birds were better oriented toward.

The homing performance, which is calculated as the ratio of the beeline "release site-target" to the flight time, is an indicator of how fast a pigeon flew to its target. Hungry pigeons did not significantly differ in their homing performance in comparison with fed pigeons in all releases with an exception of group B at the release site RB1. There, the hungry pigeons flew significantly faster to the food loft (45 km/h) than the fed pigeons flew to the home loft (30 km/h). Overall, the average flight speeds are low and indicate that some pigeons took a rest during the journey.

GPS experiment

The mean vanishing bearings of hungry and fed pigeons were significantly different (Fig. 3). For each group, the distribution of vanishing bearings at 2 km was significantly different from random (Fig. 3A, parameter r). Hungry pigeons' initial orientations can be divided into two groups: one group of hungry pigeons (2 pairs and one single bird) chose the direction toward the food loft. The other group of hungry pigeons (3 pairs) first flew south. The majority of the fed birds flew in direction of the home loft. Control pigeons (of the fed pigeons), released on a later day, were all heading south (Fig. 6).

Figure 4 shows all GPS tracks, which confirms that all pigeons flew directly to their assigned target, albeit using different routes. These were inspected in detail on Google Earth maps providing both flight paths and altitude profiles of the landscape.

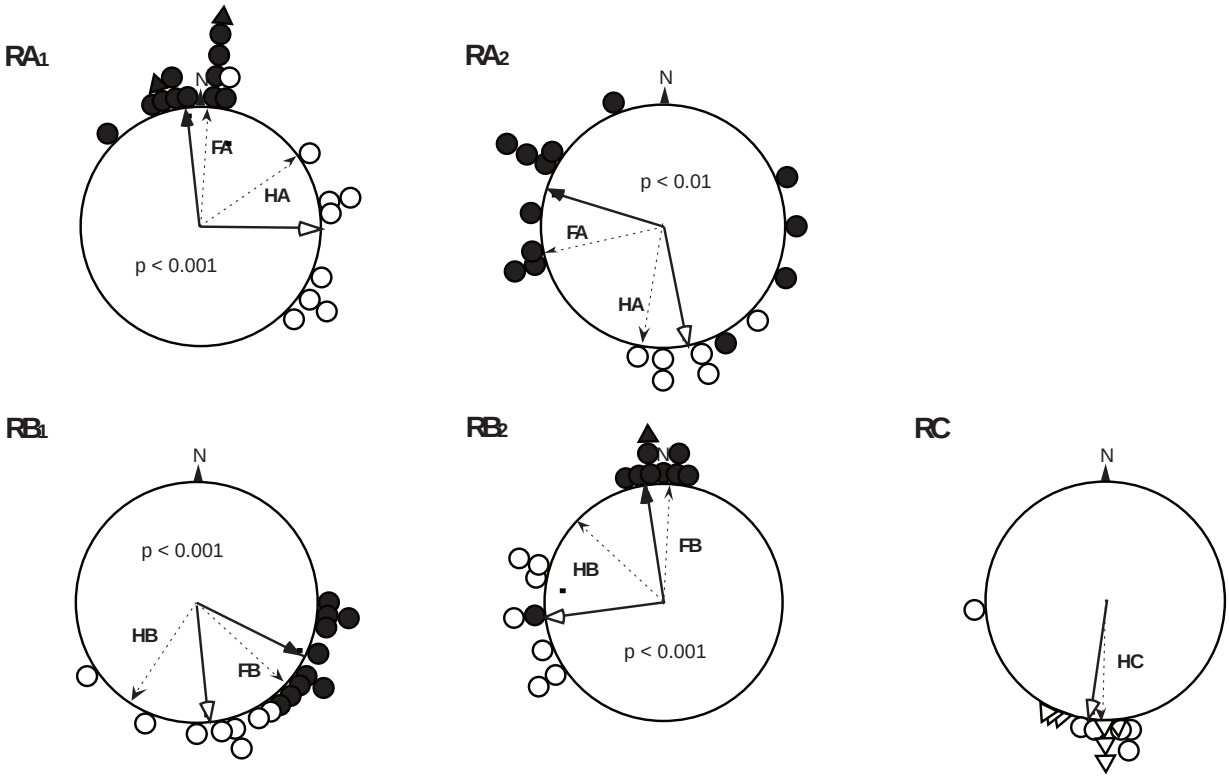

Fig. 6. The vanishing bearings of control pigeons in all releases. The control pigeons flew always to their home loft. For simplification, the direction to the lofts are depicted as HA, HB or HC when comparing with the direction of the fed pigeons (home direction) in the experimental releases and with FA, FB or FC when comparing with the direction of the hungry pigeons (food loft direction) in the experimental releases. The black circles depict pigeons that flew to their home loft which corresponds to the direction of the food loft in the experimental releases, the white circles depict the pigeons that flew to their home loft which corresponds to the direction of the home loft in the experimental releases. Circles represent pairs of pigeons, triangles single pigeons. The bold arrow shows the mean vanishing bearings of the ‚hungry' pigeons with a black arrow head and of the ‚fed' pigeons with a white arrow head, the dotted arrow shows the home loft directions. RA1, release site Mönchaltdorf with 18 ‚fed' and 24 ‚hungry' pigeons. RA2, release site Müllheim, with 12 ‚fed' and 26 ‚hungry' pigeons. RB1, release site Ellighausen, with 16 ‚fed' and 20 ‚hungry' pigeons. RB2, release site Schwägalp, with 14 ‚fed' and 19 ‚hungry' pigeons. RC, release site Bracciano, with 19 pigeons flying to the home loft but no data of pigeons flying to the food loft direction. The difference between the pigeons following either direction for each release was calculated with the Watson-Williams-F-Test for significance (see p-values within the circles).

The first group of hungry pigeons that were directed toward the food loft already at initial orientation first deviated from the beeline by following the shore of the lake Bracciano and then maintained their bearing (azimuth 230-245°) until they all reached the mountainous region (450 m a.s.l.) preventing them from seeing the coast (20 m a.s.l.). Once there, they slightly adjusted their course following valleys down to the coastal area and heading toward the familiar training corridor, following it to the food loft. One hungry pigeon flew from the release site first south but then circumvented the lake Bracciano north and northwest to the town Bracciano, where it flew a circle and then took a new direction (232°) for about 5 km. At this point it faced forested hills, took a turn south and descended 150 m along a canyon to the village of Cerveteri, from where it gradually turned to the familiar flight corridor.

The second group of hungry pigeons flew initially southward, but all changed their bearing after passing the lake Bracciano (8-10 km from the release site). One pigeon started to change its course early at the middle-eastern border of lake Bracciano and then headed toward the western hills at 242°, almost in parallel to the beeline from the release site to the food loft. One pair flew a longer distance southward but changed its course then more abruptly, heading 214° to the hills. One pair of pigeons started to change course gradually when they passed the small lake of Martignano (2 km east of the lake Bracciano), flying a long arc until they adjusted to an azimuth of 243°, again almost parallel to the beeline "release site-food loft".

All hungy pigeons aligned their flight direction at some stage roughly parallel to the original food loft direction from the release site (240°). On average, the deviation from the beeline "release site-food loft" was 6° (±6° = standard deviation, mean = 236°, 95%

confidence interval within 230-242°). An unspecific heading toward the sea would be the bearing of 216° (perpendicular to the coastal line) and this bearing is outside the confidence interval range of the observed one. Most of the birds maintained the food loft direction until they hit the second topographical obstacle, the mountainous region stretching parallel to the shoreline. After crossing or flying valleys downhill to the west, most pigeons descended to the coastal plane and followed the familiar highway A12 to the food loft. Highways have been shown to act as guiding cues in pigeon homing (Lipp et al., 2004). After feeding at the food loft, all pigeons flew back to the home loft.

The fed pigeons flew all directly south along the beeline to the home loft. Most of them reached the entrance of a valley 8 km north of the loft that led them straight home. One pair of pigeons deviated already at the release site in easterly direction and maintained that course for 20 km until they abruptly corrected their course to the west where they entered a valley leading them home. Only two pairs of pigeons missed the valley and flew to the east spending some time exploring the outskirts of Rome. They did return but from the other end of the home valley.

A quantitative analysis of the flight parameters assessed by GPS tracking is provided in Table 2. There is no significant difference between any flight parameter calculated (Mann-Whitney U-Test): vanishing time (vt), vanishing track length (vp), homing efficiency (hom ef), path efficiency (path ef), path linearity (path lin) and the mean GPS speed (speed).

Discussion

Our data show that homing pigeons have knowledge of two memorized places in relation to their own position in an unknown area, and that they make a decision where to fly to according to their motivation. In all releases, hungry pigeons departed in significantly different directions from the fed ones, and their flight times were not longer, indicating a direct flight to the target and did not need to fly home first. The GPS experiment showed that about half of the hungry birds flew straightforwardly to the food loft, while the other half flew first south and then, corrected their bearings in alignment with the initial compass direction to the food loft. The fed pigeons flew directly home. Firstly, these findings strongly support that the pigeons orient according to a map-and-compass strategy, and secondly, they imply that their navigational map is cognitive: they are able to memorize different target locations concurrently.

Vanishing bearings, homing times and GPS flight paths

We predicted that hungry pigeons would choose a different course from the fed ones if they were able to memorize simultaneously two different target coordinates and to choose between them on-site and show similar homing times. Alternatively, in the case of a navigational map consisting of one set of target coordinates only ("loftocentric" strategy), they should orient homeward first until reaching a familiar terrain to change the flight toward the food loft, and thus ought to show prolonged flight times to the target.

Precise vanishing bearings are difficult to predict because the choice of an actual flight direction is subject to release site, training and home-related peculiarities. Repeated training along a defined compass direction is known to have a significant impact on initial orientation from maritime release sites (Dell'Ariccia et al., 2009a). A good example for a training effect on the initial orientation can be seen at the release site RA_2, where the mean vanishing bearing of the hungry birds was 297° (training direction 303°) and for the fed pigeons 128° (training direction 123°). On the other hand, pigeon groups B and C did not show a training bias in their vanishing bearings. Thus, training effects were not consistent in all groups of pigeons. The topography at a release site might also influence the vanishing bearings, e.g. a mountain chain (1000 m a.s.l.) lying between site RA_1 and both lofts might have led to scattered initial orientation of the fed pigeons and causing losses. Release site specificities seem to be consistent when reviewing the mean vanishing bearings of all experimental and control releases: the deviations are all in the same direction despite the differences in training experience and loft origins. These observations can be explained by either a slight navigational error in the position-finding step caused by local factors or by topographical features that deflect the initial flight patterns.

The homing performance (hp) did not differ significantly between hungry and fed pigeons, indicating that the hungry pigeons could not have adopted a homing strategy leading them close to the home loft before reaching the familiar training corridor as expected by a "loftocentric" map. In one release (RB_1), the hungry pigeons even homed significantly faster than the fed pigeons and had also the best homeward orientation (hc = 0.91) of all releases. Nonetheless, two hungry and two fed groups showed relatively slow average homing performance (hp = 29-33 km/h), which indicates that the homing flight must have been interrupted at times. Taking rests during homing is observed when pigeons are exhausted, insecure or inexperienced.

The results from the GPS experiment not only confirmed the findings of the traditional vanishing bearing observations, but also added valuable information for interpretation of the orientation of pigeons during flight. However, flight tracks are rarely coincident with the beeline to the target, since they reflect a compromise between an initially chosen compass direction and a variety of topographic factors and individual flight strategies. In fact, the initial and maintained compass setting of one group of hungry pigeons, passing the lake Bracciano northerly, represents a rare example of directionality and path straightness, especially after repeated directional training between food and home loft.

An example for an unexpected vanishing behavior is the second group of hungry pigeons (circumventing the lake to the east): they initially followed a route coincident with the beeline to the home loft. There are three possible reasons for the vanishing behavior: a) choosing a direction toward the home loft, that is, a non-cognitive "loftocentric" strategy, b) following fed pigeons flying south toward home, and c) avoiding lake Bracciano (note that birds do not need to approach the lake very closely to change direction).

A "loftocentric" strategy and thus an initial choice of a flight direction toward the home loft is most unlikely because all hungry pigeons corrected their course already at the level of lake Bracciano or soon afterward and kept then a direction largely coinciding with the initial direction to the food loft. Most importantly, the first course corrections occurred 20 km before the home loft, thus far outside of the familiar loft region. Secondly, after correcting their initial flight bearing, all pigeons aligned their flight direction to the initial food loft direction which indicates that the pigeons did not head just for the sea (which they could have seen on the horizon). Thirdly, this alignment of the middle part of the flight tracks happened still in unfamiliar terrain with no distant cues because the pigeons faced a mountain region obstructing the view to the coastal plane with familiar beacons such as villages and the highway A12.

Following fed pigeons flying in the home loft direction is also not very likely because the GPS tracks reveal that the fed pigeons did not pause, indicating a steady and fast flight which hungry pigeons, after 5 minutes delay, possibly could not track.

The lake Bracciano was obviously a dominant obstacle because all pigeons circumvented it. Avoidance of lakes and other topographic barriers is a well-documented phenomenon (Wagner, 1972; Bonadonna et al., 1997; Dell'Ariccia et al., 2009a). One typical example is a hungry pigeon that crossed shortly the lake while flying south and changed its course at the shore of the lake, heading toward the food loft until it reached the mountain area.

Despite the different initial orientations of the two groups of hungry pigeons, we do not believe that there are birds which do have a two-target mental map versus birds that lack the ability of memorizing different goals. Rather it appears that both hungry groups tried to follow a pre-calculated direction to the food loft. An intriguing question remains: why did the hungry pigeons that avoided obstacles readjusted their flight direction not directly toward the food loft but seemed to prefer a direction in parallel to the initial beeline "release site-food loft"? Possibly, this may reflect that flying birds do not update their local position continually but in longer intervals.

The behavior of the fed pigeons was more uniform, all of them departing toward the home loft and correcting their courses 20 km after the release site toward a valley that led them home. The home loft and its surroundings are not perceivable from greater distances because the loft lies within a valley. As observed in earlier studies in this region, pigeons usually fly within a valley and not across (Lipp et al., 2004) which bears a risk of following a 'wrongly' directed valley. The two pairs of pigeons flying easterly might have missed the 'right' valley, and were flying for some time in the outskirts of the city of Rome before returning from a familiar angle into the home valley. Larger cities appear to attract pigeons temporarily in many regions, possibly by the presence of pigeon flocks.

Finally, we would like to emphasize that the results of the vanishing bearing and GPS experiments confirmed the predictions of a cognitive navigational map better than expected. The GPS-tracked pigeons have used a map-and-compass strategy as indicated by direct flight paths with recognizable course corrections. This is of considerable importance for future tracking studies assessing the sensing of geophysical or olfactory cues to establish a homing strategy.

The mental map problem

The term navigational map is subject to some confusion depending on the fields of investigation. In the field of bird migration, the presence of a large-scale navigational map is often inferred by displacement studies of migrants to a point outside their traditional routes from where they correct their course toward the migratory goal (Perdeck, 1958; Thorup et al., 2007; Chernetsov et al., 2008; Holland et al., 2009), or by tracking migratory routes following very different courses (Gill, 2009; see URL in references). It appears conceivable that migratory birds memorize both target and home coordinates, but a displacement experiment cannot prove it because it represents a case of single-target navigation. Migratory birds may have

a seasonally dependent set of coordinates, e.g. an internal clock sets the migration program and its target (Berthold, 1996). Unlike migrating birds, albatrosses do not rely on a specific compass bearing home because they forage over thousands of kilometers across the ocean (Bonadonna et al., 2005; Weimerskirch et al., 2002). However, when they home, they still have only one recognizable target for navigation, the breeding site. They may memorize other coordinates, but it cannot be ruled out that their mental map is based on their actual position and distance to the breeding site. Conceptually, single-target maps may include different levels of navigational complexity. The simplest case is that a bird just senses the difference of intersecting gradients (e.g. olfactory, magnetic) and tries to reduce the difference to home, by meandering flight paths, to the levels to which it has been imprinted until it reaches the familiar target region (Wallraff, 2005). In this case, the bird may have no mental map at all, and could return by a largely non-cognitive robot-like procedure. But the directedness of our pigeons' flight paths in the GPS study argues against this homing strategy.

A cognitive navigational map, however, includes a higher level of complexity, particularly if it involves a position determination at an unknown place. In addition, cognition involves the ability to make choices between targets according to motivation. These conditions, however, cannot be met if the navigational map of the birds contains only one set of goal coordinates. For migratory birds, this means that the displaced birds would need to be manipulated locally to induce a choice between the breeding and the wintering region, entailing bidirectional orientation according to manipulation. Likewise, albatrosses would need to be familiarized with a second target for choosing a course according to motivation. In principle, our approach of establishing a food and a home site emulated, on a smaller scale, the situation of seasonally shuttling migrants and permitted to investigate whether the pigeons were holding concurrently different sets of coordinates among which they can select a flight direction.

According to Bennett (1996), at least three requirements must be met in order to show whether animals use a cognitive map: a short-cut must lead across unfamiliar territory, familiar landmarks are not seen, and path integration is not being used. The first requirement of Bennett is clearly fulfilled by our results: from an unfamiliar location, hungry pigeons flew either directly to the food loft across unknown territories or they corrected topographically induced deviations toward the target sites in early segments of the flight. To satisfy the criterion of non-familiarity, the Swiss pigeons had even been moved for 150 km into a test region they had never experienced before. For the Italian birds, a familiar panoramic framework could have been the sea, but the birds had never been anywhere close to the release region before. Also, homing pigeons rarely forage and explore their neighborhood; they usually fly on a direct route home and stay in the vicinity of the loft with a radius of 800 m (Gagliardo et al., 2007), which minimizes the possibility that the pigeons were familiar with other areas than home. At our Italian loft, the familiar home range was larger but did not exceed 4 km and the pigeons were always trained northwest of the home loft. The training flights were also recorded with GPS (Fig. 5) and they were always confined to a narrow training corridor, far away from the release area.

The second requirement, lack of familiar landmarks guiding the pigeons in their initial choice, was clearly met, too. In Switzerland, new home lofts were established in prealpine forested hills without a clear topographic beacon. The food lofts were located in topographically variegated regions with agriculture, human settlements, hills and forests. Likewise, the release sites were situated at the same altitude as the lofts but behind mountainous regions that prevented an outlook. Only release site RB2 was at a higher altitude, but was also within a mountainous region with steep and meandering valleys with a limited vista. In Italy, the GPS tracks showed that the pigeons could indeed recognize a familiar flight corridor, since they changed direction immediately after or shortly before hitting it. However, for topographic reasons explained before, there was no opportunity to see that corridor from the distant sites where the hungry birds corrected their flight paths. Also, the home loft lies within a valley and any possible beacons are not perceivable outside the valley. Thus, visual beacons cannot explain their initial choice and course corrections, and can account only for the last part of the flights.

The third criterion of Bennett, lack of path integration, is also confirmed, although it generally plays a lesser role in pigeons. Path integration is a common strategy in animal homing that relies solely on the information gathered during the outward journey (Mittelstaedt and Mittelstaedt, 1980), but homing pigeons appear not to rely on this strategy (Wallraff, 2001). The outward journey can have some influence on the flight track of pigeons (Wiltschko and Wiltschko, 1978; Gagliardo et al., 2009). Possibly, information collected en route might have induced a small bias in initial headings of both the fed and some hungry birds toward the home loft, because the transport route followed largely the beeline from the home loft to the release site. But without any input collected during the drive, pigeons are still able to home (Wallraff, 1980). Also, path integration generally requires ac-

tive movement during the outward journey (Wehner, 1992), which does not occur when pigeons are passively transported by car.

The results of the GPS experiment are in line with a recent study on fruit bats (Tsoar et al., 2011). Fruit bats were transferred to an unknown region 44 km from their cave. Some bats flew first to a familiar fruit tree and some flew home thus also heading to different target locations from an unfamiliar terrain. In addition, recent research on spatial tasks with pigeons in a laboratory setting showed that pigeons have a sense of distance (Gibson et al., 2012) requiring cognitive spatial encoding.

Our study provides a solid support to the cognitive map hypothesis, showing consistent results under various environmental conditions and with a large number of pigeons. We conducted experiments with pigeons of different age and experience, in different geographical regions, from different release sites, and with pigeons being reared in different home lofts. It is well known that regional factors may influence the employed navigational strategy (Wiltschko et al., 1987a; Ganzhorn, 1992; Walcott, 1996) while other reports show that pigeons from different lofts may differ in vanishing bearings even when the home direction is the same (Wallraff, 1970). Finally, also differences in early experiences can influence the factors used for navigation (Wiltschko et al., 1987b).

In conclusion, our data indicate that pigeons have the ability for memorizing different target locations, and to establish a spatial relation between them and their position in an unknown territory, the essence of a cognitive navigational map. Possibly, with age and homing experience, the birds build up a mental map containing an increasing number of memorized positions facilitating efficient homing. Clearly, further studies are needed to test this hypothesis and to explore the sensory basis of this large-scale navigational map.

List of abbreviations & symbols

FA	Food loft of group A
FB	Food loft of group B
FC	Food loft of group C
HA	Home loft of group A
HB	Home loft of group B
HC	Home loft of group C
RA	Release site of group A
RB	Release site of group B
RC	Release site of group C
N	released number of pigeons
n	number of pigeons arrived at target
hc	homeward component
hp	homing performance
hom ef	homing efficiency
path ef	path efficiency
path lin	path linearity
vp	vanishing track length
vt	vanishing time
r	mean vanishing vector
α	mean vanishing bearing
δ	direction to the target
R	release site

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Chapter 2

Altered orientation and flight paths of pigeons reared on gravity anomalies: a GPS tracking study

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Summary

The mechanisms of pigeon homing are still not understood, in particular how they determine their position at unfamiliar locations. The "gravity vector" theory holds that pigeons memorize the gravity vector at their home loft and deduct home direction and distance from the angular difference between memorized and actual gravity vector. It predicts that pigeons reared in lofts either within or outside a gravity anomaly should show divergent initial orientation when released in a normal gravity area and that pigeons should show differences in their flight behavior when crossing a strong gravity anomaly. We have moved two identical mobile pigeon lofts to Ukraine. We placed one loft in a strong gravity anomaly (Bandurove) showing a north-to-south gravity gradient, and the other loft 8 km apart in a normal area but on a spot with a strong local anomaly with a gravity gradient in west-eastern direction. After training over shorter distances, pigeons were released from a gravitationally and geomagnetically normal site 50 km north in the same direction for both home lofts, requiring them to cross a massive gravity anomaly to home. As expected by the theory, the pigeon groups showed divergent initial orientation: the birds for which the gravity gradient coincided with the beeline to the loft were much better homeward oriented and returned without problems, while the pigeons grown up on a gravity gradient perpendicular to the home direction showed prolonged disorientation and returned poorly. In addition, some of the GPS-tracked pigeons also showed changes in their flight paths when crossing gravity anomalies. We conclude that even small local gravity anomalies at the birth place of pigeons may have the potential to bias the map sense of pigeons, while reactivity to gravity gradients during flight was variable and appeared to depend on individual navigational strategies and frequency of position updates.

Introduction

The mechanisms of long-distance orientation of birds are only partially understood. According to the map- and compass theory by Kramer, the orientation process consists of two different parts [1]: a position-finding mechanism, and different mechanisms to determine and maintain directions. The latter include solar [2], stellar [3-4] and magnetic cues [5-6], landscape features [7-9], polarized light patterns [10-11] and possibly, infrasound cues [12].

The position-finding mechanism, the map sense, is still unclear. Until now, two not mutually exclusive types of maps have been proposed: mosaic maps and gradient maps [13-15]. A mosaic map consists of experienced cues in a spatial frame, and is therefore mostly restricted to a familiar area (also called a familiar topographical map). Potential cues for a mosaic map are distinct visual landmarks [16-20] and airborne odors [21-22]; the latter also providing information about distant locations. On the other hand, a bi- or multicoordinate gradient map should have stable gradients and therefore should be extendable to unfamiliar areas. Potential candidates for a large-scale gradient map are olfactory cues and parameters of the earth's magnetic field.

An olfactory gradient map is thought to consist of a global grid formed by intersecting relative proportions of atmospheric factors allowing for homing and navigation by minimizing the difference of locally perceived versus remembered values at the home loft. A strong argument in favor of the olfactory hypothesis is that olfactory deprivation strongly interfered with homing and navigation [23-26]. One counter-argument is that the effect of olfactory deprivation was not related to navigation and that olfaction plays a role in activating the bird's navigational system [15,27], a conclusion challenged by Gagliardo and colleagues [28] on the basis of GPS tracking.

The earth's magnetic field has also been considered as a candidate for a bicoordinate map formed by inclination angle and intensities of the geomagnetic field [5,14-15]. Many studies have experimented with disrupting the magnetic sense of pigeons by attaching magnets [29-31] or Helmholtz coils onto the birds' heads [32-33] but they failed to show a consistent effect on pigeon homing. Also long-distance navigation in albatrosses wearing toggling magnets on their head was not affected [34]. Releasing pigeons at local magnetic anomalies have shown some effects but again, the results and interpretations differ in these studies as homing itself is not severely affected [35-38]. Magnetic cues are subject to strong temporal and geographic variations. This casts some doubts whether they form the evolutionary backbone of a global positioning system for long-distance navigators [15, 39-40].

Taken together, there is agreement that the navigational system of pigeons reflects the interaction of several mechanisms maintaining directions, but there is large disagreement about the mechanisms underlying the map sense. At least at present, it would seem that none of the proposed olfactory and magnetic

mechanisms has the necessary robustness to account for the precision of avian long-distance navigators.

Surprisingly, gravity itself as a principal cue for the orientation process has barely been considered. Larkin and Keeton [41] have found a significant correlation between the pigeons' mean vanishing bearings and the day of the lunar synodic month, suggesting that subtle changes in gravitational forces may influence navigation. Dornfeldt [42] conducted a thorough multivariate analysis of pigeon homing in relation to geomagnetic, gravitational, topographical and meteorological cues. He concluded that the most important factor accounting for poor homing orientation and performance was gravity anomalies. Kanevskyi and colleagues [43] followed pigeons by helicopter flying over a massive tectonic break (associated with a gravity anomaly). The pigeons altered their flight paths when crossing the anomaly and also showed some telemetrically assessed changes of the EEG. Conceptually related to the gravity vector theory, Köhler [44] proposed a navigation mechanism by assuming that the pigeons were able to use the visual horizon line for perceiving the difference between the horizontal plane at the home loft and the release site. On the other hand, Lednor and Walcott [45] released homing pigeons within weak negative gravitational anomalies (salt domes) but could not find a correlation with the homing orientation.

One theory explaining the possible use of gravity parameters for navigation is the 'gravity vector' hypothesis proposed first by Kanevskyi [43]. It claims that pigeons are imprinted to the gravity vector at their place of birth, and that this information is stored as a neuronal memory independent of the perception of the actual gravity vector. This would represent an analog to a mechanical gyroscope, which maintains the original inclination of the gravity vector plus the orthogonal horizontal plane after displacement. Thus, at any given point, a gyroscope permits comparison of the angle between a virtual (memorized) and an actual gravity vector converging in the center of the geoid. The comparison of two such vectors with their orthogonal horizontal planes allows for computing azimuth and distance to the point of departure. For a displaced pigeon, this implies that it always senses, under normal gravity conditions, the approximate home direction and distance. It may then find home by either using a map-and-compass strategy with the support of geomagnetic, solar and topographical cues, or it may use a gradient strategy constantly monitoring memorized versus actual gravity vector and reducing the difference. Obviously, such strategies are not mutually exclusive.

In general, the gravity vector theory predicts that pigeons should sense small irregularities of the normally smoothly changing gravity vector. Such irregularities of gravity vector inclinations are found in massive gravity anomalies where they manifest themselves as changes in the horizontal component of the gravity vector. Thus, when pigeons are released from such anomalies, they might deviate from the optimal compass direction for some distance because the birds miscalculate their position in relation to home. During flight, one may also expect occasional directional changes of the flight direction depending on the frequency by which pigeons are assessing the vector differences.

At present, the only approach to experimentally assess the impact of variations in the inclination of gravity vectors on navigation behavior is to study the flight paths of birds near or over strong gravity anomalies. Therefore, during the past four years, we have conducted in the Ukraine a series of studies aimed at elucidating the orientation behavior of pigeons encountering massive gravity anomalies. The Ukraine was chosen because its central part contains massive and well-mapped gravity anomalies distributed in a predominantly flat countryside without any long-distance visual cues. In this paper, we describe a first study with the goal of verifying two predictions made by the vector gravity theory.

In this study, we investigated the orientation behavior of homing pigeons reared within and outside a gravity anomaly and their flight behavior when crossing a gravity anomaly. Thus, we placed one loft in a strong gravity anomaly and another 8 km apart, in a gravitationally normal area as judged by low-resolution gravity maps (scale 1:200'000). We randomly assigned breeding pairs of local origin to one of the lofts and raised the pigeons under identical conditions. When high-resolution gravity maps (scale 1:10'000) became available, we realized, however, that the loft in the anomaly-free zone had been placed on a very small but strong local anomaly, the gravity gradient running at right angle to the gradient present at the other loft. For the experiment, the offspring birds from the two lofts were released together from an unfamiliar test site 50 km to the north, from where the beelines to both lofts were almost identical and then had to cross the Bandurove gravity anomaly for 10 to 15 km to home. The gravity theory would predict (i) that pigeons reared in lofts in which the gravity gradients would coincide with the home direction would be better oriented than those whose home loft had a gravity gradient perpendicular to the gravity gradient pointing homeward, and (ii) that pigeons crossing the gravity anomaly should show changes in their direction during flight.

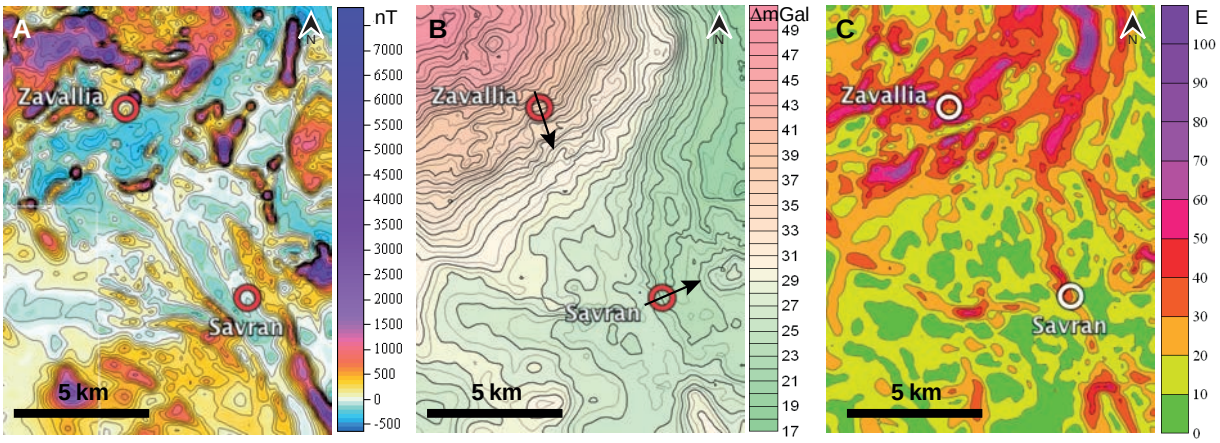

Fig. 1. Magnetic and gravity anomalies around the pigeon lofts. The location of the pigeon lofts, Zavallia and Savran, are indicated with a circle. (A) Magnetic anomaly map (nT = nanoTesla). (B) Gravimetric anomalies, the change of the gravity intensity (ΔGB – Bouguer, mGal = milligal). Arrows show the direction of the gravity gradients. (C) Horizontal gravity gradients (E = Eötvös), highest values mark locations with steepest gradient of gravimetric values in border zones of gravimetric anomalies. Note the location of the Savran loft (S-pigeons) on a small yet steep gravity gradient in east-west direction characterized by elevated E-values. For a photographic map illustrating the topography of the area see https://www.dropbox.com/sh/2yrhdtcyzt5uu99/ZFJeNJb0lk.

Materials and methods

Pigeons and loft situation

Two Swiss military pigeon lofts were transferred from Switzerland to Ukraine. One was placed in a village called Savran (N 48°8', E 30°4'), in a near-normal gravity field (Fig. 1) as evidenced by survey maps. These pigeons are referred to as S-pigeons (Savran-pigeons). After having obtained high-precision geophysical maps, however, we noticed that this loft has been placed on a locally small yet strong irregularity of the horizontal component of the gravity vector (30-40 E), the gradient aligned in a west to east direction (Fig. 1C). For geophysical definitions, see paragraph 'Topographic and geophysical maps' below. The other loft was placed in Zavallia (N 48°11', E 30°0'), only 8 km north in a gravity anomaly, which differed, on average, by 30 mGal from the normal zone (Fig. 1B). These pigeons are referred to as Z-pigeons (Zavallia-pigeons). The horizontal gradient was aligned approximately in a north-south direction, and was of equal strength as the one at Savran (30-40 E), even though the gravity values were much stronger in Zavallia. The Z-loft was located 1 km from a hill formed by material from a graphite mine of 100 m altitude, and which was visible for humans from a radius of approximately 10 km. We bought 60 pigeons from pigeon breeders from a different region and assigned randomly half to each of the lofts. As soon as the fledglings were ready to fly they were trained in all cardinal directions around the loft up to 15 km. Early in the training phase, we mounted PVC dummies on the pigeons' back to accustom them to the weight and the size of a GPS logger. The PVC dummies stayed on the pigeons for the whole training period. The GPS loggers were from Technosmart (version GiPSy2) and recorded the position of a pigeon every second with an average accuracy of 4.2 m (in 95% of fixes). The last training release was recorded with GPS loggers. For the Z-pigeons, the training release site was 15 km northeast of their home loft. For the S-pigeons, the training release site was 15 km west of their home loft.

Experimental releases

The experimental release site Pologi (N 48°34', E 29°43') was chosen on the basis of having the same homeward direction for both lofts: the Z-loft, 46 km apart, and the S-loft, 54 km apart, outside the Bandurove anomaly (Fig. 2). Since the theory expects that pigeons should derive positional information from the angular difference in gravity vectors between release site and loft, the Z-birds should not experience conflicts with their home gradients (even when these are anomalous) as long as the beeline to the loft coincides with the gradient direction. On the other hand, an imprinted (distorted) orientation of the gravity vector at the home loft might cause a conflict at a release site if it diverges from the home gradient. Before the experiment, we transported the pigeons by car at night to the release site and let them rest a minimum of 4 h until sunrise. Then, we mounted the GPS loggers onto the pigeons' back and released them individually in alternating order, a pigeon from home Z-loft and then a pigeon from home S-loft. We released in total 12 Z-pigeons and 14 S-pigeons on different days, in August 2010, to compensate for possible meteorological variations, and because the number of GPS was not enough to use on all pigeons within one day. We kept 5-minutes intervals between releases to prevent

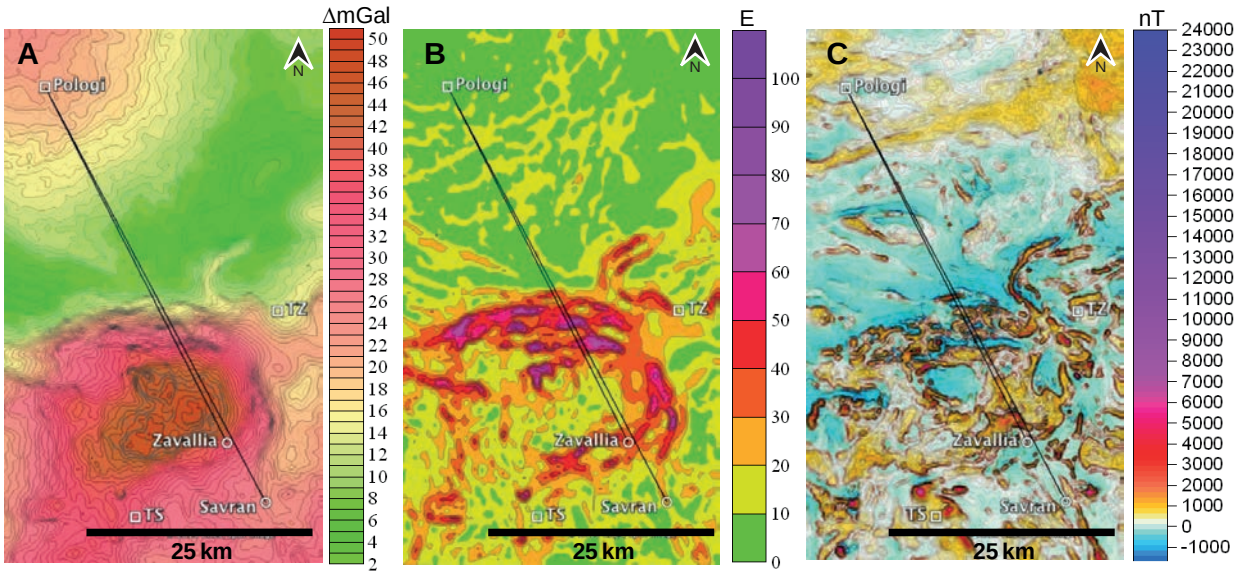

Fig. 2. Gravity and magnetic anomalies of the test region crossed by the pigeons. (A) Gravimetric anomalies, the change of the gravity intensity (ΔGB – Bouguer, mGal = milligal); (B) Horizontal gravity gradients (E = Eötvös), highest values mark locations with steepest gradient of gravimetric values in border zones of gravimetric anomalies. (C) Magnetic anomaly map (nT). The square symbols indicate the release sites: Pologi, the experimental release site; TZ, the last training flight to Zavallia loft and TS, the last training flight to Savran loft. Black lines indicate beelines from Pologi to the Z- loft (46 km) and S-loft (54 km).

pigeons from following each other. After the return of the pigeons to their home lofts, we collected the GPS loggers and downloaded the data to the computer with GiPSy2 software (Technosmart).

Analyses

Vanishing bearings, vanishing time and flight track parameters were calculated using the freeware Wintrack [46]. We determined vanishing bearings at a distance of 2 km and 5 km from the release site which is in accordance with previous literature [47]. Similarly, the vanishing time (vt) is the time a pigeon flew around the release site until it was 2 km from the release site. A difference between the two groups of pigeons in vanishing time was analyzed with the non-parametric Mann-Whitney-U-test. With the statistical software Oriana (Kovach Computing Services) the mean vanishing direction (α) and length of the vector (r) were calculated. The mean vanishing vector length (variable between 0 and 1) is a reciprocal measure of angular dispersion [48]. Its projection onto the axis of the homeward direction gives the homeward component (hc) showing how homeward orientated the whole group of pigeons was. The Rayleigh-test indicated whether the vanishing bearings had a uniform distribution. The Watson U2-test was performed to reveal any difference between the groups and the Watson-Williams F-test to depict a difference in the mean vanishing bearings. In order to investigate the orientation behavior after initial orientation, the pigeons' dispersal behavior after release was examined. Here, we included the analysis of dispersal behavior after initial orientation from 5 to 30 km at steps of 5 km. We determined the distance of the flight track from the beeline "release site-home loft" (beeline R-H) at the above mentioned distances from the release site which were drawn as radii of circles with the release site as the middle point of the circles. Therefore, the length of the dispersal distance (dd) from the beeline R-H is the line connecting the intersection beeline-circle with the intersection flight track-circle. The dispersal distance has positive values when being east of the beeline R-H and negative values when being west of the beeline R-H (the beeline R-H points from north to south). The distance of 30 km was determined as the maximum distance point because 6 of the tracks of the S-pigeons were incomplete and no values were recorded by the GPS loggers for further distances. We compared the dispersal distances of the tracks of the two groups for each distance from the release site with the T-test using the freeware R.

The analysis of flight tracks parameters aimed to show differences in the general flight behavior between the S- and the Z-pigeons. The following parameters were calculated from the flight tracks: homing performance (hp), path efficiency (path ef), homing efficiency (hom ef), path linearity (path lin) and GPS speed. Homing performance was calculated by dividing the beeline distance R-H by the duration of the flight (km/h) and is an indicator of how fast and straightforward the pigeon flew to its home loft. Path efficiency is a similar measure but takes into account the whole track length instead of the time; it is the beeline distance between the release site and the home loft divided by the track length in %. Homing efficiency adds the homeward component as percent-

age of the track with a homeward component > 75%. Path linearity is the sum of the ratio "distance between two positions 32 s apart and the track length of two positions 32 s apart" in % and shows how straight the pigeon's tracks were regardless of the home direction. The GPS speed is the ground speed in km/h excluding rests. The parameters between the two groups were analyzed for any difference with the Mann-Whitney-U-test.

In addition, a second analysis was conducted to compare the flight behavior of the pigeons just before the anomaly, when crossing the border zone of the anomaly with a steep change in the horizontal gradient of gravity and when flying within the anomaly. The same flight tracks of the experimental release were used, but only of the Z-pigeons because most of the S-pigeons did not cross the anomaly. Three zones were defined with a width of 3 km each: zone 1 corresponding to the non-anomalous area in front of the anomaly, zone 2 corresponding to the border zone of the anomaly and zone 3 corresponding to the core anomaly area. Flight parameters such as the flight duration (in minutes), path efficiency (path ef), path linearity (path lin) and GPS speed were calculated for each part of the pigeon's flight track within the three zones. First, a non-parametric repeated measures analysis of variance by ranks, the Friedman-test, was used for each parameter. If the test showed a significant difference in the means of a parameter, we then used the Wilcoxon signed-rank test to compare the flight parameter in the different zones.

Of the 12 released Z-pigeons, 12 vanishing bearings and 11 flight tracks could be used for analysis. One GPS track was excluded because it did not record the full flight path. Of the 14 released S-pigeons, 11 vanishing bearings and 4 flight tracks could be used for analysis. Three S-pigeons were lost and 6 were late returners (>5 h) of which none had a fully recorded flight path. One flight track was excluded but only in the flight parameter analysis (n=4) because it was an outlier, overshooting the home loft and continuing a long journey south of the home loft (the track is depicted in Fig. 5B).

Topographical and geophysical maps

Flight tracks were visualized with the aid of QGIS. Geophysical maps present Bouguer gravity anomalies obtained by gravimetric terrestrial surveying. Bouguer anomalies are typically corrected for latitude, topographical elevation above sea level and soil thickness, and are expressed in Δga (indicated as Δ mGal in Figures and simply as mGal in the text). The modulus of horizontal gravity gradients was calculated by using the Bouguer anomaly data: gravity difference in neighboring points, divided by the distance between these points. The gradient is usually measured in units of Eötvös (E). One E corresponds to 0.1 mGal/km. There is thus a strong correlation between Bouguer maps and horizontal gradient maps: high values of E occur in the border zones of strong gravity anomalies (Fig. 1 and 2). Figuratively, these zones indicate regions wherein the vertical direction of a plumb is slightly tilted toward a laterally situated underground inclusion or lack thereof, whereas in the center of a gravity anomaly, the direction of a plumb coincides with the theoretically expected direction to the center of the earth.

Gravity maps include different levels of resolution. Those in Figure 1 (loft placements) and Figure 7 (Sekretarka region) are largely based on a grid of 100 x 100 m with an accuracy of 0.1 mGal. The other maps were composed from terrestrial surveys including cell grids of 250 x 250 m, 250 x 500 m, and 500 x 500 m. Magnetic maps were composed from aerial (50 m altitude) and terrestrial surveys (observation lines of 100 or 250 m distance, respectively). The contour interval on the maps of the magnetic field is 50 nT (Fig. 1, 2 and 9).

The frame of the gravity gradient map shown in Figure 6 denotes the changes in the horizontal gradient from 0 to 50 E with an abrupt variation on the northern border of the anomaly. The average Bandurove gravimetric amplitude, which is the difference between the value at the center of the anomaly and the mean anomaly in the environmental field, is 30 mGal. The amplitude from different sides of the anomaly is 40 mGal from the north, 35 mGal from the west, 28 mGal from the east and 20-13 mGal from the south. The release site Pologi shows a magnetic intensity of 329 nT, the Z-homeloft area in the village Zavallia 384 nT and the S-homeloft area in the village Savran 206 nT (Fig. 1A).

Ethics Statement

The experiments were conducted according to Swiss regulations on animal welfare and experimentation, licenses 99/2008 and 92/2011 issued by the Zurich Cantonal Veterinary Office. The above government licenses are only issued after having been approved by an ethics committee including scientists and animal protection organizations. The approval is not shown to the applicants (who apply directly to the government). Keeping homing pigeons and conducting pigeon releases in the Ukraine does not need governmental permission. Homing pigeons are not an endangered or protected species. Pigeon racing is a popular sport as in many other countries worldwide, including the US, all European and many Asia countries. The lofts were placed on private grounds on a rental basis with the permission of the landlords.

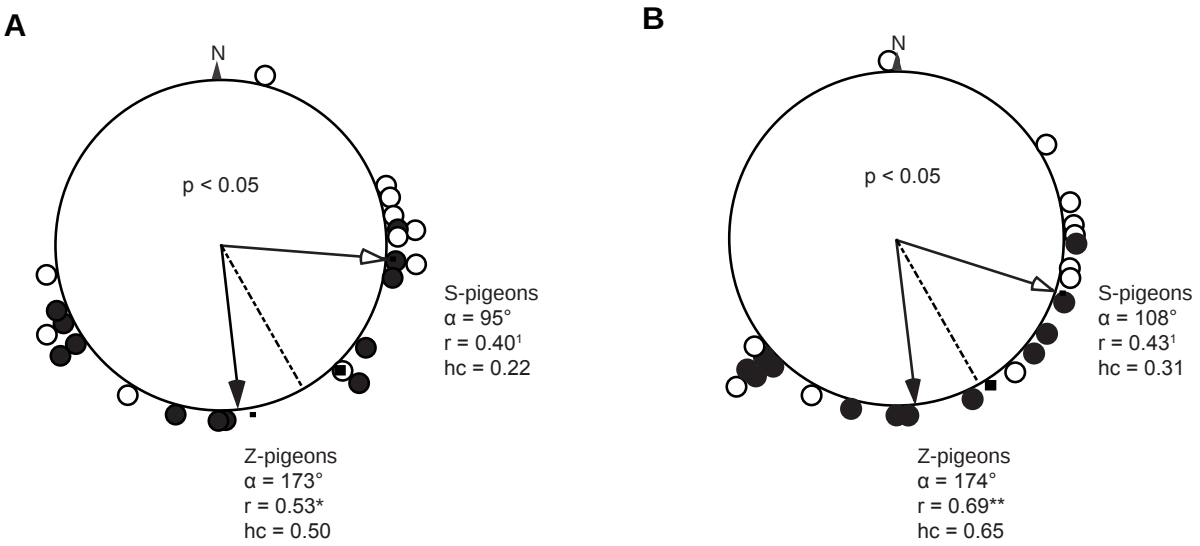

Fig. 3. Vanishing bearings of Z- and S-pigeons at 2 and 5 km. (A) Vanishing bearings of Z- and S-pigeons at 2 km and (B) at 5 km from the release site. The black dots refer to Z-pigeons (n=12) whereas the white dots refer to S-pigeons (n=11). Each symbol is one pigeon. The bold arrows show the mean vanishing bearings of the Z-pigeons with a black arrow head and of the S-pigeons with a white arrow head. The dotted line shows the home loft direction, 152°. α is the mean vanishing bearing, r is the mean vanishing vector and hc is the homeward component. The difference between vanishing bearings of the Z- and the S-pigeons was calculated with the Watson-Williams-F-Test for significance (p-values within the circles). The significance levels for the Rayleigh test (r) are indicated with [1] = not significant, * = p<0.05, ** = p<0.01.

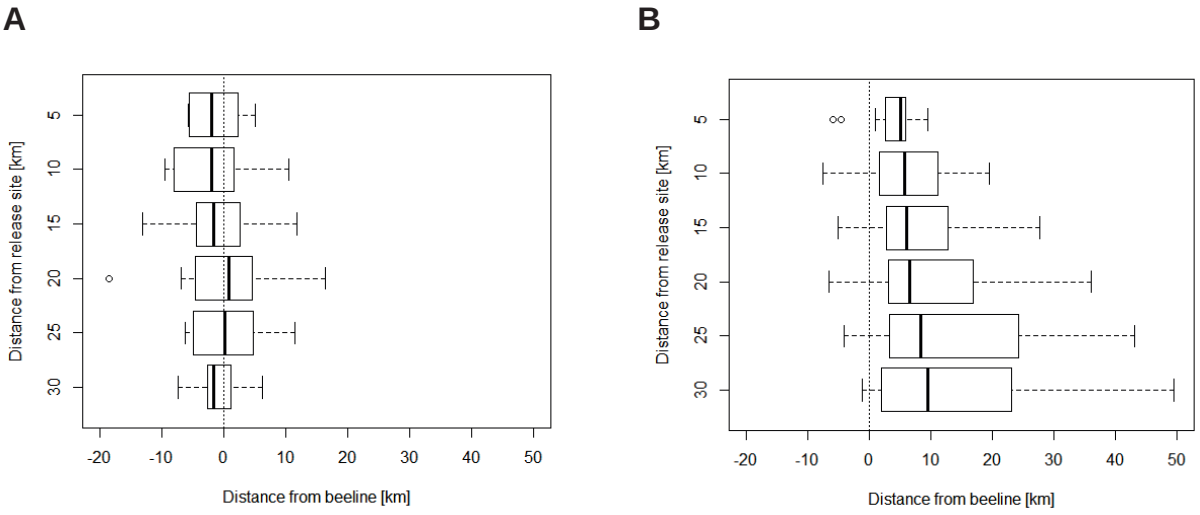

Fig. 4. Pigeons from the two lofts maintain different flight directions. (A) Distances of the Z-pigeons from the beeline at 5 km steps. (B) Distances of the S-pigeons from the beeline at 5 km steps. Points easterly of the beeline release site-home loft (R-H) correspond to positive values of the x-axis, whereas points westerly of the beeline R-H correspond to negative values. The box ranges show the upper and lower quartile with the median, and whiskers extend to the most extreme data point no more than 1,5x the interquartile range. Points outside the range are outliers.

Results

Comparison of pigeon groups

All Z-pigeons (n = 12) arrived at the home loft and were continuously homeward oriented. In contrast, S-pigeons (n = 14) were not homeward oriented and showed poor homing performance: we lost 3 pigeons and 6 were late returners (>5 h).

The S-pigeons showed a significant poorer initial orientation compared to the Z-pigeons and the vanishing bearings of the Z- and the S-pigeons were significantly different from each other (Fig. 3). The distribution of the vanishing bearings of the Z-pigeons was significantly different from random (parameter r, Fig. 3A). Whereas the vanishing bearings of the S-pigeons showed a random distribution (parameter r, Fig. 3A). The mean vanishing bearing of the S-pigeons deviated from the home direction by 57° ±SD 77°. Many S-pigeons headed first north and northeast. The S-pigeons spent also more than double the time flying

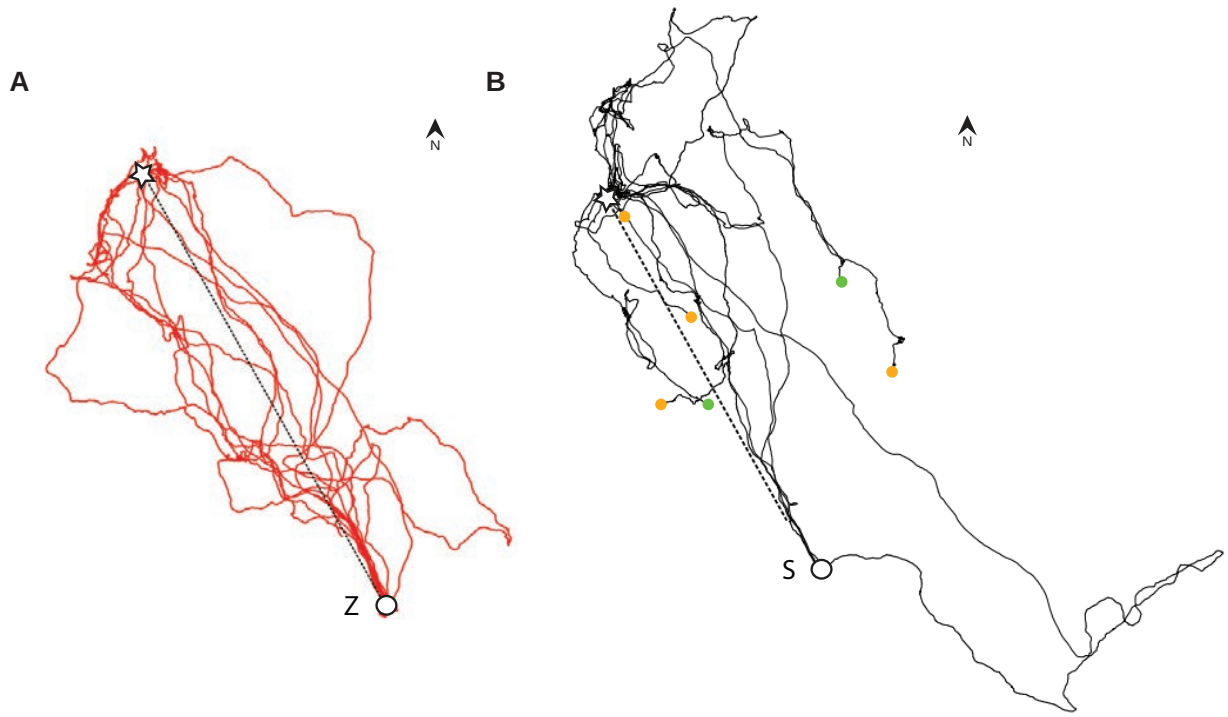

Fig. 5. Flight tracks from the experimental release site Pologi. The dotted line is the beeline from the release site, indicated with a star, to the home lofts. (A) The flight tracks of 12 Z-pigeons flying to their home loft Z (Zavallia). The distance from the release site, to the home loft Z is 46 km. (B) The flight tracks of 11 S-pigeons flying to their home loft S (Savran). The distance from the release site to the home loft S is 54 km. An orange dot indicates that the pigeon stopped flying and was pausing until the GPS ran out of battery power. A green dot indicates that the pigeon was still flying when the GPS ran out of battery power.

(vt) around the release site within 2 km distance than the Z-pigeons but the difference is not significant (S-pigeons vt mean: 11.1 ±SD 12.4 min, Z-pigeons vt mean: 4.7 ±SD 4.3 min).

The poor initial orientation of the S-pigeons did not change when examining their vanishing bearings at 5 km distance from the release site. At 5 km, the vanishing bearings were still not different from random (parameter r, Fig. 3B). The mean vanishing angle still deviated from the home direction by 44° ±SD 75°. In contrast, the Z-pigeons were better oriented at 5 km compared with the results at 2 km with a higher homeward component and a stronger mean vanishing vector (parameter r and hc, Fig. 3B). The difference between the mean vanishing vectors of the two groups was also significantly different at 5 km distance from the release site.

The pigeons not only differed in their initial orientation but dispersed continuously at distances up to 30 km from the release site (Fig. 4). The positions of the S- and Z-pigeons at 5, 10, 15, 20, 25 and 30 km distance from the release site were significantly different from each other (T-test, $p<0.05$ for all). The number of Z-pigeons is always 11 for all distances; for S-pigeons it is 11 up to 15 km, at 25 km there were only 10 and at 30 km 9 birds. The S-pigeons showed a strong bias toward the east: the median of all distances lies always eastern of the beeline R-H (positive values in Fig. 4B) and the scatter of the data increased with the distance from the release site. The Z-pigeons scattered the most at 15 to 20 km distance from the release site but then converged again when approaching the home loft (Fig. 4A).

Figure 5A depicts the flight tracks of 12 Z-pigeons (but only 11 tracks were used for analysis): the homing performance was 51 km/h and they flew with an average speed of 69 km/h. The path efficiency was 72% and an average of 71% of the track was homeward oriented with a path linearity of 94%. In Figure 5B, 11 flight tracks of S-pigeons are illustrated, but 6 flight tracks are incomplete and stop (indicated with yellow and green points). In total, we calculated flight track parameters of 4 S-pigeons that returned home: they did not differ significantly from the Z-pigeons in homing performance (40 km/h), homing efficiency (58%), path efficiency (62%) and GPS speed (68 km/h, Mann-Whitney-U-test). However, the S-pigeons flew significantly more tortuously than the Z-pigeons with a path linearity of 90% ($p<0.05$, Mann-Whitney-U-test).

Analysis of tracks within the Bandurove anomaly

The flight tracks of the Z-pigeons superimposed on a scheme of a horizontal gravity gradient map are depicted in Figure 6. The comparison of the flight behavior of the Z-pigeons before crossing the border of

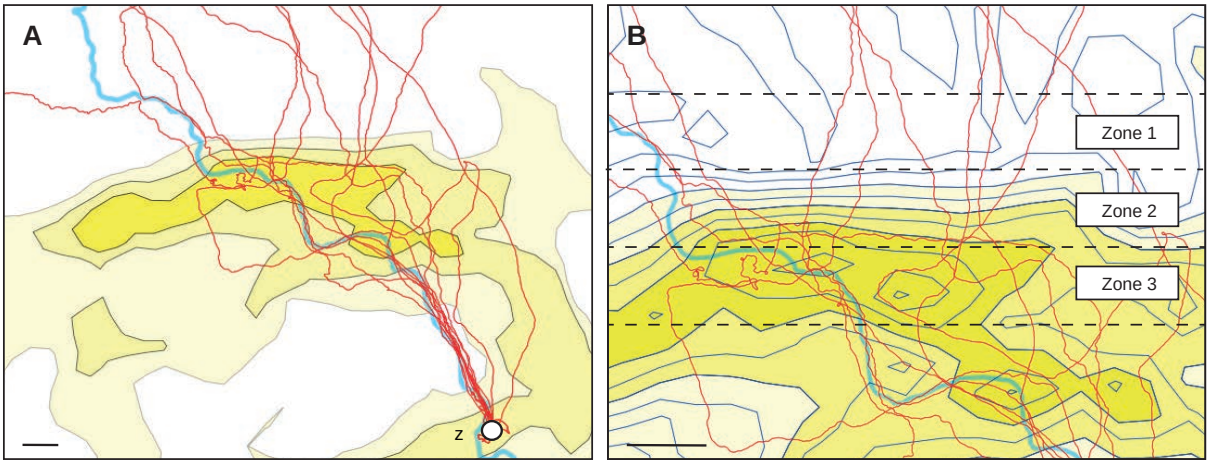

Fig. 6. Flight tracks of Z-pigeons crossing the Bandurove anomaly. (A) Flight tracks of 11 Z-pigeons. Z depicts the home loft. The thick meandering blue line is the Bug river. The contour lines of the gravity anomaly (horizontal gradient) are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (E = 20), middle (E = 30), dark (E = 40). 1 E = 0.1 mGal/km. (B) Close-up of the same map but with blue contour lines in steps of 5 E. Zone 1: normal gravity area before the Bandurove anomaly; zone 2: gravity anomaly area with a steep change of the horizontal gravity gradient (isolines are close together); zone 3: the core anomaly area with continous values of 40-50 E. The bar in the lower left corner of both pictures represents 3 km.

the anomaly and flying within the anomaly revealed following results: comparing the means of each flight parameter (path efficiency, path linearity, GPS speed and time) with the Friedman-test showed only a significant difference of the path linearity between the zones ($p<0.05$). The Wilcoxon signed-rank test revealed that significant differences could be attributed to the comparison of the parameter between zone 2 and zone 3, and zone 1 and zone 3 ($p<0.05$ for both). There was no difference between zone 1 and zone 2, i.e. the flight tracks became more tortuous only within the core anomaly (zone 1 path lin = 98 ±SD 1.7%, zone 2 path lin = 98 ±SD 1.4%, zone 3 path lin = 97 ±SD 2.5%). All other parameters were not significantly different tested with the Friedman-test. Path efficiency was 83% (±SD 11.3%) in zone 1, 78% (±SD 15.0%) in zone 2, and 66% (±SD 31.2%) in zone 3. The GPS speed was 66 km/h (±SD 12.3 km/h) in zone 1, 65 km/h (±SD 11.5 km/h) in zone 2, and 66 km/h (±SD 12.2 km/h) in zone 3. The flight time was 3.4 min (±SD 0.9 min) in zone 1, 4.2 min (±SD 2.6 min) in zone 2, and 5.9 min (±SD 3.9 min) in zone 3.

Inspection of individual flight tracks within the gravitational anomalies

When investigating more closely the individual flight tracks of the Z-pigeons, most of them showed more tortuous flight paths within the core of the Bandurove anomaly area, at 18 km northwest of the home loft (Fig. 6). One individual bird, after crossing the border zone of the anomaly, abruptly changed its southerly flight course to the west for 4 km, then to the south for 4 km, just to turn to the east, shaping a square with its flight course. Another example of a bird changing its flight course within the anomaly, was a pigeon flying southwest, then changed abruptly to southeast, but then, after 5 km, changed to fly northeast for 5 km, circled and then flew south, homeward. Two birds started following the river already before the anomaly, one of them suddenly flying four small circles within the core anomaly, the other following the river closely until it reached the home loft. Nine out of 11 pigeons aligned to the river 8 km north of the home loft that led them directly home.

Among the S-pigeons, one bird showed a peculiar behavior (outlier, Fig. 5B). The pigeon departed rapidly with high speed (>80 km/h in easterly direction, changed the course after 5 km in southeasterly direction (139°) and continued straightforwardly with high speed for 75 km, thus missing the home loft. It then suddenly reduced flight speed to 40-50 km/h, and turned in a right angle toward north-east, into a region containing numerous gravity anomalies (the Sekretarka region, Fig. 7B). It then adopted a tortuous flight course passing in-between two gravity anomaly peaks and maintained that course until it hit another gravity anomaly where it turned 180°, flying back in the direction it came from. Upon approaching the anomaly region passed before, the bird changed the course apparently aligning to the contours of the gravity anomaly (Fig. 7C), thereby flying around a former missile station for intercontinental rockets. afterward, it made again a sharp turn and flew 40 km NW to reach the home loft. The Sekretarka region contained also a localized magnetic anomaly peaking up to 10’000 nT (Fig. 7D). Yet the flight track aligned much better with the border zones of the gravimetric anomaly.

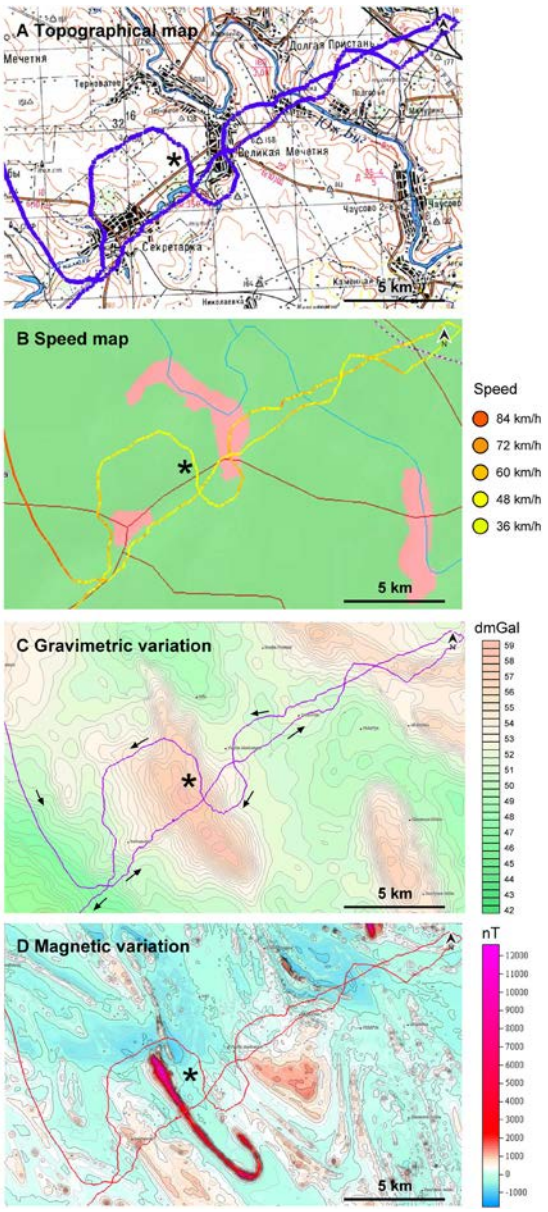

Fig. 7. Flight path of a pigeon crossing gravitational and magnetic anomalies. (A) Topographical map of Sekretarka region. (B) Map showing flight speed of pigeon 305. Note the sudden reduction in speed when approaching the anomaly. The reduced flight speed is maintained throughout the region. (C) Gravimetric anomalies. Densely spaced isolines indicate those regions with irregularities of the horizontal gravity gradient. (D) Strong magnetic peak on top of the gravitational anomaly. Asterisk denotes the position of a former Sovjet SS-18 rocket launch station.

Inspection of training flights

Given the unexpectedly poor performance of the S-pigeons, we analyzed carefully the flight paths of both Z- and S-pigeons during their last training flights in order to check for a directional bias at the experimental release site.

The last training release of the Z-birds occurred 15 km NE of the Z-loft under conditions when they could have easily seen the artificial hill marking the position of the home loft by taking the beeline direction of 200° (Fig. 8). Instead, they all deviated westerly from the beeline, following initially a flight path (225°) along the steepest gravimetric gradient (coincident with high E values, Fig. 8A). Approximately at the level of the same Bouguer levels as their home loft, they began to turn south, eventually following the Bug river for another 5-7 km to their home loft. Flight tracks coincide much less with the 3D topography of the magnetic anomaly since the pigeons crossed several magnetic peaks close to the release site (Fig. 8B). Looking at the initial vanishing behavior of the experimental release site Pologi, we found 4 tracks for which a training bias might account for (mean vanishing vector at the training site: 224°).

On the other hand, the tracks of the training flights of the S-pigeons revealed a much more variable pattern (Fig. 9). The initial vanishing orientation was random with a mean vanishing vector pointing north (348°). Three birds flew first in western direction for 4 -5 km, then turned and flew directly home. Five pigeons headed northward toward the Bandurove anomaly, of which only one pigeon corrected the flight course homeward. Four S-pigeons, however, showed long journeys from 40 to 120 km within or even beyond the Bandurove anomaly. These four pigeons differed in their flight behavior at the experimental release because only one of them flew home in a direct course. Due to widely differing initial orientation during the training flight, there was clearly no directional bias at the release site.

Discussion

Pigeons reared in lofts located on gravity anomalies with diverging horizontal gravity gradients showed, as theoretically anticipated, a significant difference in their vanishing bearings from the same release site in a normal gravity area. The Z-pigeons were significantly homeward oriented while the S-pigeons showed random orientation. Furthermore, the S-pigeons were not only initially disoriented, but also showed prolonged disorientation up to 30 km from the release site and some pigeons never found back home. The few S-pigeons that did home did not differ in their flight behavior to the Z-pigeons that homed all successfully. The Z-pigeons that crossed the anomaly did change their flight behavior within the anomaly in comparison of a 3 km zone in front of the anomaly. Within the core gravity anomaly, they showed more tortuous paths. Thus, both a specific (initial orientation) and a general prediction (reactions to anomalies) of the gravity vector theory were fulfilled. However, we realize that the results might be subject to different interpretations. We will thus discuss first the problems of initial orientation, then reactions to gravity anoma-

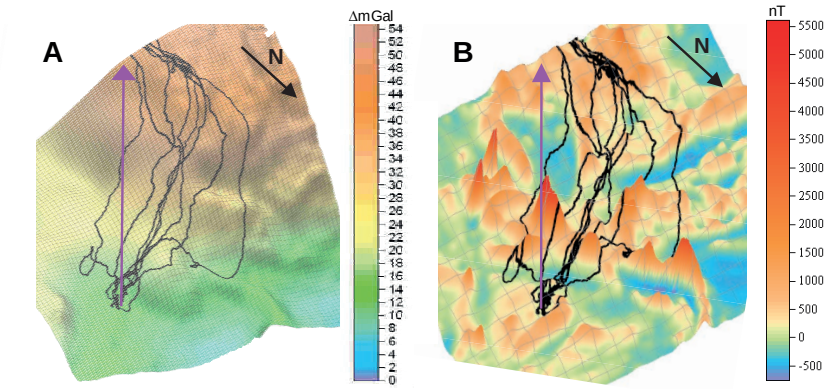

Fig. 8. Last training release of Z-pigeons northeast of the Zavallia loft. (A) Flight tracks on gravity anomaly map. Most birds appear to follow the steepest gravity gradient of the anomaly, then turn left when they hit the Bug river. Scale 0-54 Δ mGal. (B) Flight tracks on magnetic anomaly map, showing partial coincidence of magnetic and gravity anomalies. Scale -500-5'500 nT. Violet arrow shows home direction. For a topographical map of the tracks see: https://www.dropbox.com/sh/2yrhdtcyzt5uu99/ZFJeNJb0lk.

lies and, finally, the relation of gravity and geomagnetic anomalies.

Initial orientation

The initial orientation of pigeons is subject to release site specificities, training effects, and home loft conditions. The release site was in an open field in a flat topography, the next village 1.5 km to the northeast. The distribution of the vanishing bearings of the S-pigeons was random, but 6 pigeons flew to the east, in the direction of the gradient characterizing the position of the home loft. One possible explanation may be the influence of a directional training [49]. However, the pigeons had not been trained in one specific direction but in all cardinal directions. Therefore only the last training release could have had an effect on their vanishing behavior. Yet, as shown in the description of the training flights, the initial orientation at the training site was very scattered and only two S-birds flew both at the training and the experimental release site to the east. As for the Z-pigeons, the mean vanishing vector was close to the homeward direction and only 3 pigeons vanished in the previous training direction, therefore also diminishing the effect of training on initial orientation. The third and possibly most important explanation for vanishing bearings of homing pigeons is the location and the condition of the home loft. Our two lofts were exactly identical, two former Swiss army lofts, populated with comparable numbers of pigeons, both placed in a garden with an outlook within a village and fed the same diet. Both pigeon groups had similar training experience and were trained always by the same person. Thus, it appears unlikely that this type of loft-specific factors affected the results.

However, studies have shown that pigeons from a given loft have a consistent directional bias at different release sites [50-51, 47]. For example, pigeons from neighboring lofts showed divergent vanishing bearings at the same release site [51-53]. The latter study is of relevance to our data as it compared the vanishing bearings of sibling pigeons raised outside and within a magnetic anomaly, and being released at various magnetic anomalies. The birds raised in the anomaly were significantly disoriented at one site but not at other sites. Walcott speculated that the birds from the two lofts had developed different map-forming strategies in accordance with their early experience with geophysical parameters. This seems to be the most likely explanation for our data, with the exception, however, that the birds raised in the gravity anomaly seemed to be much less disturbed by variations of gravity parameters than those outside of the anomaly. The surprisingly poor initial orientation and the tracks observed during the training flight from 15 km suggest that several S-birds had experienced a problem in establishing a navigational map, while the Z-birds were mostly well oriented during both training and experimental release. This conclusion is supported by the observation that the flight tracks of the S-pigeons continued to be misdirected up to 30 km. It might be a coincidence that the different vanishing bearings reflected the diverging horizontal components of the gravity vector at the home lofts, but one cannot rule out that the small local gravity anomaly (horizontal gradient) at the S-loft with gradients perpendicular to those of the Z-loft was contributing to the orientation problem of the S-birds. However, if true, this would imply that extremely subtle differences in orientation of the horizontal gradient of gravity might produce a loft-specific bias in flight bearings at release sites. Clearly, this observation must be verified by releasing pigeons from lofts with normal gravity conditions at places located in the border zone of gravity anomalies and thus biasing the initial orientation of the birds.

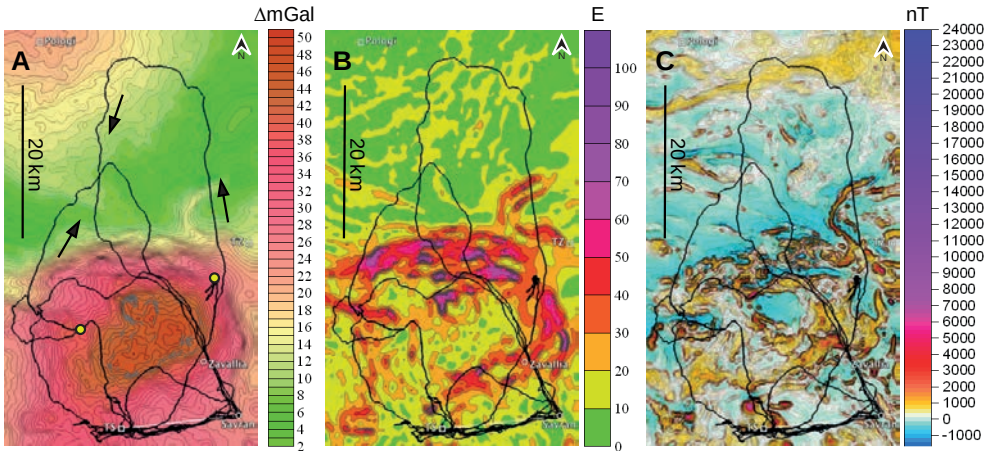

Fig. 9. Last training release of S-pigeons west of the Savran loft. (A) Flight tracks on map of gravimetric anomaly, i.e. the change in gravity intensity. Yellow dots indicate birds resting more than 5 h. Three pigeons made long journeys to the north into the anomaly and back. Arrows show flight direction. (B) Tracks on a map showing irregularities of the horizontal gravity gradient (corresponding to the steepest gradients of gravimetric values). (C) Same tracks on a map with geomagnetic anomalies. The overall geomagnetic variation is relatively low (between -1000 and 1000 nT), with scattered peaks of higher intensity. For a terrain map see: https://www.dropbox.com/sh/2yrhdtcyzt5uu99/ZFJeNJb0lk.

Crossing the gravity anomaly

The flight course of pigeons is affected by many factors. However, their effect also depends on which navigational strategy the bird applies [54-55]. Looking at individual tracks is necessary to interpret the results in a meaningful way instead of drawing conclusions only from group analysis with combined data of all tracks. In our experience, gathered during the last 10 years, one individual flight strategy is called "compass flight", in which a pigeons flies in a straight line neither paying attention to distracting topographic stimuli as villages and rivers, nor to geophysical anomalies. In our data, some pigeons adopt a straight directional flight at a high flight speed between 70-80 km/h shortly after the release site. Another flight strategy is when pigeons maintain a slower search-type flight pattern and are either guided or distracted by external factors such as landscape features, other pigeons and possibly also geophysical cues. This flight pattern is often associated with prolonged rests. Such birds are more likely to follow gravity gradients or magnetic isolines but often not exclusively. Some of flight tracks suggest that the birds sense gravity anomalies during the flight, although they do not appear constantly guided by gravity variations. The analysis of the flight tracks of the Z-pigeons approaching the Bandurove anomaly from the north showed 3 compass flyers crossing the anomaly at high speed, yet even these showed a minor flight correction in the border zone of the anomaly. The other more slowly approaching birds did not immediately react when crossing the steep horizontal gradient of the gravity vector but about 3 minutes later, when flying within the core anomaly: they showed more tortuous flight paths and sometimes abrupt changes in their flight course, e.g. one pigeon turned from flying south to flying northeast and another pigeon altered its southerly course to heading to the west, to the south and back to the east, all within the anomaly. Probably the sudden change of the perceived gravity vector when crossing the anomaly from the north irritated the pigeons and led to a search behavior indicated by greater path tortuosity. Two pigeons started following the river already within the core anomaly, possibly perceiving familiar olfactory cues from the river. Other pigeons followed the river later, after the anomaly, 7 km in front of the home loft. The last training release for the Z-pigeons also showed that approaching the Bandurove anomaly from the east itself did not cause problems. Instead of taking the direct route to the loft along the beeline, the pigeons followed the steepest gravity gradient to the southwest and then aligned their flight course to the river. Normally, flight tracks over flat countryside scatter equally to the left and right of the beeline, but there was only one bird flying initially to the left of the beeline and even this one corrected the flight path to the right side of the beeline.

There were two other examples suggestive for sensing gravity anomalies. The first observation was the behavior of the S-birds during their last training flight. Almost half of these pigeons (5 out of 13) appeared to be attracted by the northerly lying anomaly, notably devoid of any distinct topographic features. In case of a non-systematic problem of initial orientation, one would have expected that at least some birds would be heading also southward, but none of them did so. The second example was an S-bird that flew first with high speed along a (wrong) compass direction, despite of the fact that he had visited the area two days before. It changed its flight path and

flight behavior suddenly after having passed the loft. As shown in Figure 7, the bird appeared to sense a gravito-magnetic anomaly easterly of its flight path. Notably, this anomaly appears barely on large-scale maps but on high-precision maps, the gradients from the bird's position to the anomaly were as high as the Bandurove anomaly (about 40 E difference), associated with a local geomagnetic anomaly peaking at 10'000 nT. Possibly, the gradients were reminiscent of the familiar Bandurove anomaly near the birds' homeloft. On its way back, the pigeon circumvented the gravity anomaly rather precisely along the gravity isolines, before eventually turning home. Since it followed the contours of the gravity anomaly about 1.5 km before the sudden peaking of the magnetic anomaly, on might at least tentatively conclude that this location possessed some highly distinct geophysical properties. That the pigeon also circumvented a former intercontinental missile silo might be coincidence, but given the reliance of cruise missiles and adversary rockets on gyroscopic (i.e., gravity vector) information, that place was at least well chosen by the constructors.

Gravity and geomagnetic anomalies

Gravity anomalies caused by underground densities containing magnetite frequently overlap with magnetic anomalies. For example, geomagnetic anomalies have been reported to influence the flight paths of GPS-tracked pigeons [36] in a manner similar to what has been partially observed by us: namely having a preference of aligning or crossing at right angles strong anomaly gradients. Interestingly, in Dennis's study, the correlation between geomagnetic and gravity anomalies was significant ($r = 0.62$).

In order to avoid the concurrent influence of magnetic and gravity anomalies, Lednor and Walcott [45] investigated the orientation behavior of pigeons flying from the center of gravity anomalies located over salt domes with less density and therefore producing a negative gravity anomaly with little magnetic variation. The amplitudes of the anomalies ranged from -2 to -10 mGal, suggesting that gravity differences in this order have less or no impact. In comparison to the salt domes, the Bandurove gravity anomaly is positive and much stronger with ranges from 20 to 40 mGal. Perhaps more importantly, this anomaly is also more massive, caused by a tectonic break with locally interspersed magnetic and gravity anomaly peaks. One should also note that the gravity vector theory does not predict altered vanishing bearings from the center of anomalies but expects deviations from the home direction primarily for releases from border zones of anomalies.

In agreement with our observations, Dornfeldt [42] compared weaker (-9 to 14 mGal) gravity anomalies to stronger gravity anomalies (15 to 49 mGal) and found that pigeons were significantly less homeward oriented and homed slower from the stronger gravity anomalies. Supported by an extensive and detailed multivariate analysis including geomagnetic variation, topography and weather conditions, he concluded that gravity parameters form an essential part of the pigeon's map sense.

In our study, there were a few small magnetic anomalies around both home lofts but not much variation at the release site Pologi and within the Bandurove gravity anomaly, e.g. the intensity difference from the release site 2 km in the home loft direction is as little as -16 nT. This value is generally considered as geomagnetic noise. Thus, it appears unlikely that the differences in initial orientation of Z- and S-pigeons were caused by geomagnetic variations.

Conclusions

1. Our data largely fit the predictions made by the theory formulated by Kanevskyi [43], namely that birds reared in locations with different gravity gradients show different initial orientation and temporary changes in flight tracks when encountering sudden massive changes in gravity gradients.

2. The GPS tracking data from this study confirm Dornfeldt's earlier observations of altered vanishing bearings of pigeons at release sites with gravity anomalies [42], and are in line with the study of Larkin and Keeton on effects of lunar cycles on vanishing bearings [41].

3. It remains likely that at least some of the altered orientation of pigeons at release sites with geomagnetic anomalies reported by other studies may have been caused by gravity anomalies. Thus, it would seem advisable to provide gravity maps systematically for release studies aimed at assessing geophysical and other parameters.

4. Upcoming studies should further investigate whether releases at strong positive or negative gravity anomalies, with and without accompanying geomagnetic anomalies, can confirm the observed problems in orientation of pigeons, specifically misleading cues provided by gravity gradients.

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Author contributions

Conceived and designed the experiments: HPL, VK. Performed the experiments: NB. Analyzed the data: NB, SG, HPL. Provided geophysical maps: SG. Wrote the manuscript: NB, HPL. Training of pigeons and revision of the manuscript: VM.

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Chapter 3

GPS tracking of homing flights of pigeons released within a circular gravity anomaly not associated with geomagnetic disturbances

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Summary

Successful homing occurs when pigeons know their position and set a compass home. The gravity vector theory postulates that the birds set their home course by comparing the imprinted gravity vector at the loft with the local gravity vector at the release site. However, if the pigeons are updating their position sporadically or continuously according to their memorized gravity vector, they should change course when encountering irregularities of the gravity vector. Depending on the frequency of "position fixes", they might then either correct course gradually home, or maintain altered flight directions over longer distances.

In this study, we released pigeons from the centre of the Boltischka circular gravity anomaly, a pure gravity anomaly with no magnetic anomalies. In the centre of the anomaly, the gravity vector does not show horizontal deviations whereas in the border zone of the anomaly there is a strong change in the horizontal component of the gravity vector. In comparison, we released control pigeons from a site with no associated gravity or magnetic anomalies equidistant from the home loft (91 km). We predicted that the birds' initial orientation was not different in comparison to control pigeons. But as the pigeons would fly over the border zone of the anomaly, they would show changes in their flight course. By and large, the predictions were met: the pigeons within the anomaly showed a slightly scattered orientation at 2 km distance but were homeward oriented at 5 km just before crossing the border zone of the anomaly and did not differ in their bearings compared to the control pigeons. But after having crossed the border zone of the anomaly and encountering a second gravity anomaly located in the beeline to the loft, a number of birds changed their flight direction, maintaining the wrong course over long distances, whereas the control pigeons showed a significantly less dispersed pattern of flight tracks converging toward the loft. However, we also lost numerous birds from both sites without having any information of their tracks. Thus, the data are (conservatively) biased by analyzing successful homers only.

Introduction

The gravity vector theory predicts that pigeons should sense small irregularities of the normally smoothly changing gravity vector, such irregularities being able to redirect a pigeon's flight. Such irregularities of gravity vector inclinations are found in the border zone of massive gravity anomalies where they manifest themselves as changes in the horizontal component of the gravity vector (= horizontal gravity gradient). Our first study in Zavallia and Savran provided first experimental evidence supporting this claim. However, gravity anomalies are likely to overlap partially with geomagnetic anomalies, and separating the influence of gravity anomalies from that of geomagnetic anomalies is difficult. Thus, in this study, we released homing pigeons from within a circular gravity anomaly showing normal magnetic values. The Boltischka gravity anomaly was formed by a meteorite impact in the early Mesozoic era (Entin, 2011), which caused a crater of about 25 km diameter, filled up with less dense material, and located in a flat countryside. This geological situation causes on one hand negative gravity intensity values (-36 mGal) and on the other hand, in the border zone, strong deviations in the horizontal component of the gravity vector (55 E). The shape of the gravity anomaly is fully circular, ensuring that pigeons must cross the anomaly along any flight direction chosen. Control pigeons from the same loft were released from a site southeast of the anomaly, equidistant to the loft. The home loft was located in Novoukrainka, 91 km from both sites. We released the pigeons either at the anomaly or the control site on the same days. We did not expect a different initial orientation of the pigeons released within the anomaly as the centre of the anomaly does not show a change of the horizontal gravity gradient. However, when the pigeons cross the border zone of the anomaly, they experience a tilted gravity vector that might lead to an adjustment of their flight course. Hence, we predicted

(i) that the vanishing bearings of pigeons released in the centre of the Boltischka gravity anomaly should not be different from those of the control pigeons, and

(ii) that pigeons crossing the border zone of the gravity anomaly should show changes in their flight direction as compared to the control birds.

Materials and methods

Pigeons and loft situation

We placed a former Swiss military pigeon loft in Novoukrainka (N 48°16', E 31°30'), outside of the town. The topography around the area is flat with no visible beacons such as hills, high towers and coastlines. The loft was populated with pigeons from local pigeon breeders one year earlier. The pigeons we used were mixed in gender, most of them were 1 to 2 years old with little flight experience, a few were 3-4 years old

Picture 1. Swiss military pigeon loft placed outside Novoukrainka in Ukraine.

Picture 2. Typical flat landscape in Ukraine.

provided by the local pigeon breeder caring for the loft. All pigeons were trained up to 20 km in flock and afterward in pairs and then singly up to 60 km from the east. Early in the training phase, we mounted PVC dummies on the pigeons' back to accustom them to the weight and the size of a GPS logger. The PVC dummies stayed on the pigeons for the whole training period. The GPS loggers were from Technosmart (version GiPSy2) and recorded the position of a pigeon every second with an average accuracy of about 4 m in 95% of the fixes.

Maps

The presented maps show gravity anomalies either expressed as difference in intensity of the vertical component in mGal to the normalized (Bouguer) gravimetric values as obtained by aerial surveys (= gravimetric map or vertical gradient map), or they depict the horizontal component of the gravity vector that is, the horizontal change in the gravitational acceleration vector from one point on the earth's surface to another (= horizontal gravity gradient map). This is customarily measured in units of Eötvös (E). One E is 0.1 mGal/km. Contour lines are in interval levels of 5 E. The Boltischka gravity anomaly (width: 25 km), is the greatest anomaly in the area (see supplementary Figure S1). Southwest of the circular anomaly are smaller arc-shaped anomalies with values of 30 E. Another way to image the gravity anomaly is showing the change of the intensity of the vertical gravity vector (Bouguer anomaly). Due to less dense material within the Boltischka crater, the gravity intensity levels are negative within. The congruency of the two gravity anomaly maps lies in the border zones. Therefore, we sometimes showed the tracks of the pigeons superimposed on a gravity intensity map that gives a nicer and more precise illustration of the anomaly. The magnetic anomaly map shows the intensity of the earth's magnetic field in nT (= nanoTesla, see supplementary Figure S2). Contour lines show intervals of 10 nT. In the Boltischka area, there is no concurrence of magnetic anomalies with gravity anomalies.

Experimental releases

We released pigeons within the Boltischka circular gravity anomaly (N 48°56', E 32°14'), 91 km northeast of the home loft. The control release site was 31 km southeast to the release site (N 48°44', E 32°31') and also 91 km distant from the home loft. The direction from the experimental release site and from the control release site to the home loft were 217° and 236°, respectively. We released 26 pigeons from the anomaly of which 18 returned to the home loft (70%) and of which 17 tracks were recorded. We released 28 pigeons from the control site of which 16 returned successfully (57%) and of which 15 tracks were recorded. In addition, we planned to release each pigeon at both, the control and the anomaly site but due to the losses, in the end we had GPS tracks of only 8 pigeons from both release sites. After the releases from within the anomaly and from the control site, we released 5 pigeons northeast, i.e. 4 km behind the circular anomaly at Ivanka, 111 km distant from the home loft (N 49°4', E 32°23').

The evening before the experiment, two cars transported the pigeons to both release sites. The crates with the pigeons were placed on top of the car with view of the surroundings. Before sunrise, the crates were placed in an open field and the start of the pigeon releases was coordinated with a person at the other release site to have similar flight times. The pigeons were released singly with 5-minute intervals between releases. We conducted the same procedure on 5 days in July and August 2011 because of limited number of GPS devices. We started releasing at 5.30 am because the daily temperature rose very quickly after sunrise to above 30° C which increased the risk of pigeons resting in a tree during the day to avoid flying during the heat. The air temperature was around 17° C at time of release, only on the last day, the tem-

Picture 3. GPS logger attached with velcro tape to a pigeon's back.

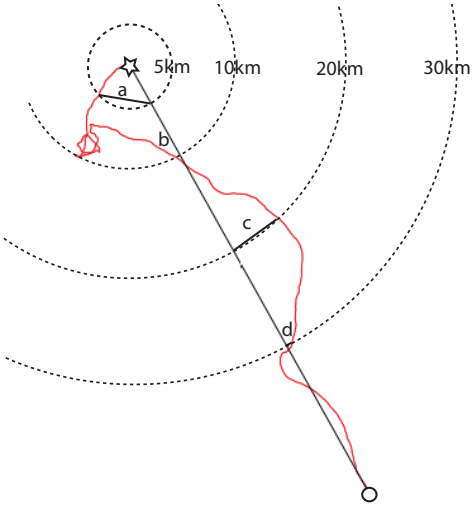

Fig. 1. Determination of the distances of the flight track from the beeline "release site-home loft" at specific intersections. The pointed quarter-circles indicate the distance to the release site, marked with 5 km, 10 km, 20 km and 30 km. The star is the release site, the circle the home loft, connected by a beeline. The letters *a* to *d* show the length of the line connecting the intersection "beeline-circle" with the intersection "flight track-circle".

perature dropped to 12° C. The weather was on all days clear with no wind apart from the fourth release day where the clouds covered up to 60-80% of the sky during release. After the return of the pigeons to the home loft, we collected the GPS loggers and downloaded the data to the computer with GiPSy2 software (Technosmart).

Analyses

The initial orientation behavior of the pigeons at the release sites was investigated analyzing different vanishing parameters. Vanishing bearings are traditionally referred to the direction a pigeons is heading after release until it is out of sight. This term originated in early homing pigeon experiments when the pigeons' flight direction was determined when the pigeon vanished out of sight, being observed with binoculars, which was generally at a distance of 2 km. As GPS technology has substituted the binoculars, researchers analyze the heading of the pigeon still at 2 km or else otherwise stated but obviously 'vanishing' is not correct. However, the term itself is still used, sometimes with the attribute 'virtual' but here, we will name the initial flight direction as vanishing bearing. The distributions of the vanishing bearings at the different release sites were tested with the Rayleigh-test to show whether the pigeons where oriented toward one direction. The Watson U2-test was performed to demonstrate any difference between the groups (control vs. anomaly release) and the Watson-Williams-F-test to depict a difference in the mean vanishing bearings. With the statistical freeware Oriana (Kovach Computing Services) the mean vanishing direction (α) and length of the vector (r) were calculated. The mean vanishing vector length (variable between 0 and 1) is a reciprocal measure of angular dispersion (Batschelet, 1981). Its projection onto the axis of the homeward direction gives the homeward component (hc) showing how homeward orientated the whole group of pigeons was. The deviations (δ) of the vanishing bearings to the home loft direction of each pigeon was calculated and all deviations of both groups of pigeons were plotted together on a circle with the homeward direction normalized to 0°. Vanishing times until the pigeons were 2 km distant from the release site were calculated and differences between the two groups of pigeons was analyzed with the Mann-Whitney-U-test.

In order to investigate the orientation behavior after initial orientation, the pigeons' dispersal behavior after release was examined (Fi. 1). The length of the dispersal distance was determined as the distance of the flight track from the beeline "release site-home loft" (R-H) at distances from 5 to 75 km from the release site, which were drawn as radii of circles with the release site as the middle point of the circles. The dispersal distances from the beeline were calculated as absolute values. We compared the dispersal distances of the tracks of the two groups for each distance from the release site with the Mann-Whitney-U-Test. As 8 out of 25 pigeons were flying from both release sites, we also tested them exclusively with the Wilcoxon signed-rank test for pairs.

Furthermore, we analyzed flight track parameters of both groups to show possible differences in the general flight behavior. The following parameters were calculated with the freeware Wintrack (Wolfer et al., 2001): path efficiency (path ef), homing efficiency (hom ef), path linearity (path lin) and GPS speed. Homing efficiency is the beeline distance between the release site and the home loft divided by the track length in %. Path efficiency adds the homeward

component as percentage of the track with a homeward component > 75%. Path linearity is the sum of the ratio "distance between two positions 32 s apart/ the track length of two positions 32 s apart" in % and shows how straight the pigeon's tracks were regardless of the home direction. The GPS speed is the ground speed in km/h (without rests, i.e. speed < 5 km/h). The parameters between the two groups were analyzed for any difference with the Mann-Whitney-U-test.

Of 17 recorded GPS tracks from the anomaly site, we could use 17 for vanishing bearing and vanishing time analysis and 16 for the flight parameter analysis. One track was excluded because it showed many errors for position-determination. Of 15 recorded GPS tracks from the control site, we could use 14 for vanishing bearings and vanishing time analysis. One pigeon paired with another pigeon while flying and therefore we calculated the two as one data point. The 14 tracks from the control site could all be used for the flight parameter analysis. For the calculation of the flight parameter homing efficiency (hom ef) three tracks from pigeons released from the anomaly (n=13) and two tracks of pigeons released from the control site (n=12) could not be used because the tracks ended outside of the home loft area.

Results

In summary, pigeons released from the control site were initially better oriented toward the home loft than pigeons released from within the gravity anomaly at 2 km. The orientation of the pigeons released within the anomaly changed already after 5 km: they were homeward oriented and did not show a difference in their vanishing bearings in comparison to the control pigeons. However, after crossing the borders of the circular gravity anomaly, the pigeons dispersed widely and were flying for over 30 km at significantly greater distances from the direct beeline from the release site to the home than the control pigeons. The second, smaller arc-shaped anomaly also seemed to influence the pigeons' flight path. We also lost 8 pigeons that were released from within the anomaly and 12 pigeons that were released from the control site.

Initial orientation

Pigeons released in the centre of the gravity anomaly showed a scatter in their headings (Fig. 2A). Most pigeons were oriented toward southwest (home loft direction) but others disappeared northwest and two pigeons headed to the east. However, already after 5 km, their orientation improved and the majority of the pigeons were flying in the direction toward home (Fig. 2B). The analysis revealed that the pigeons showed a significantly different vanishing behavior compared to the pigeons released at the control site at 2 km distance from the release site (Fig. 2A, p-value within the circle, Watson-Williams-F-test). The Rayleigh-test revealed a slightly non-uniform distribution with a $p = 0.053$. The pigeons were not homeward-oriented at all, indicated by the low homeward component (hc = 0.38). In contrast, already at 5 km distance from the release site and still within the gravity anomaly (not crossing it yet), the pigeons were significantly oriented ($p<0.001$, Rayleigh-test) and were homeward-oriented (hc = 0.63). There was also no difference between the mean vanishing vectors of both groups at 5 km distance from the release site (Fig. 2B, p-value within the circle, Watson-Williams F-test).

Pigeons released at the control site were all heading in the same direction and after 5 km, they were closer aligned to the home direction (Fig. 2A and B). The control pigeons showed a highly significant uniform distribution of their vanishing bearings ($p<0.001$, Rayleigh-test) and were highly homeward-oriented (hc = 0.80) which improved at 5 km (hc = 0.91). The flight times (vt) at 2 km distance from the release sites were not significantly different comparing both release sites (vt, anomaly = 6.4±6.0 min, vt, control = 4.9±3.4 min, Mann-Whitney-U-test).

Crossing the border zone of the gravity anomaly

Most pigeons flew perpendicular to the gravity contour lines, crossing the borders of the anomaly in a direct flight path. Two pigeons crossed the border to the southeast, one flew a circle of 2.5 km width exactly within the steepest range of the anomaly, the other flew a circle of 1 km width within the border zone (Fig. 3). Another pigeon flew initially north, changed after crossing the anomaly to northwest and then, flew parallel to the beeline from the release site to the home loft (Fig. 4). Three pigeons crossed the border in the exact homeward direction but then changed afterward to a bearing of 192°, flying more southerly for 30 km, distancing themselves from the home course.

The flight tracks after the anomaly

It is striking that many pigeons from the anomaly showed a dispersing flight behavior and overshooting the home loft to the south or the west. Three pigeons released from within the gravity anomaly were flying over 200 km around the area and paused until the battery of the GPS ran out (Fig. 4, flight tracks with orange points at the end). Many pigeons vanished out of the anomaly in the homeward direction but then turned south, toward the second arc-shaped anomaly and corrected only later toward home. The pigeons flying north of the beeline seemed even more disoriented, flying great distances.

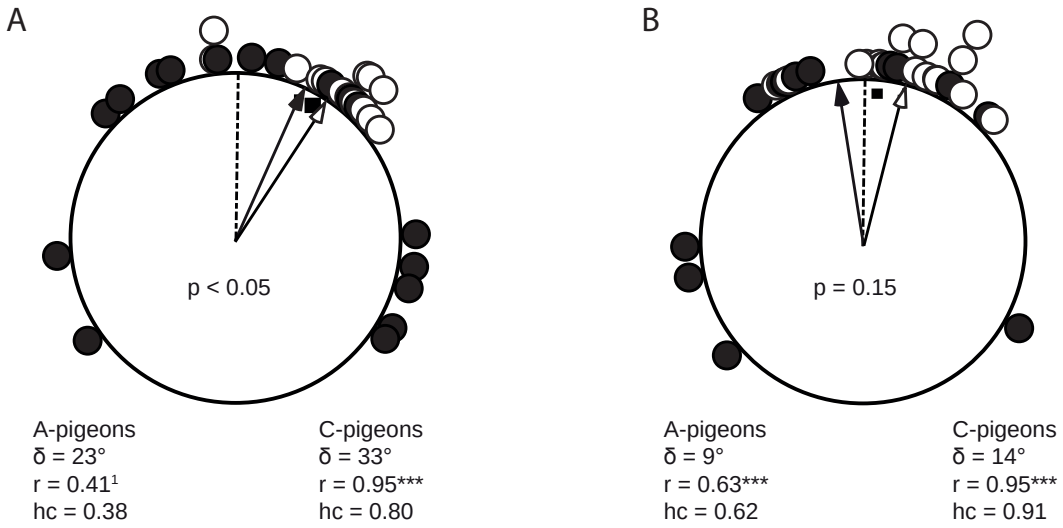

Fig. 2. Initial orientation of pigeons released in the centre of the Boltischka anomaly and at the control site. A) The position of the pigeons 2 km from the release site. B) The position of the pigeons 5 km from the release site. The black circles refer to A-pigeons (n = 17) whereas the white circles refer to C-pigeons (n = 14). Each symbol is one pigeon. The bold arrows show the deviations of the mean vanishing bearings of the A-pigeons with a black arrow head and of the C-pigeons with a white arrow head. The dotted line indicates the home loft direction, which was normalized for both groups, showing the vanishing bearings as deviation from the homeward direction. δ is the deviation of the mean vanishing bearing from the homeward direction, r is the mean vanishing vector and hc is the homeward component. The difference between vanishing bearings of the A- and the C-pigeons was calculated with the Watson-Williams-F-Test for significance (see p-value within the circle). The significance levels for the Rayleigh test (r) are indicated with [1] = p = 0.05, *** = p < 0.001.

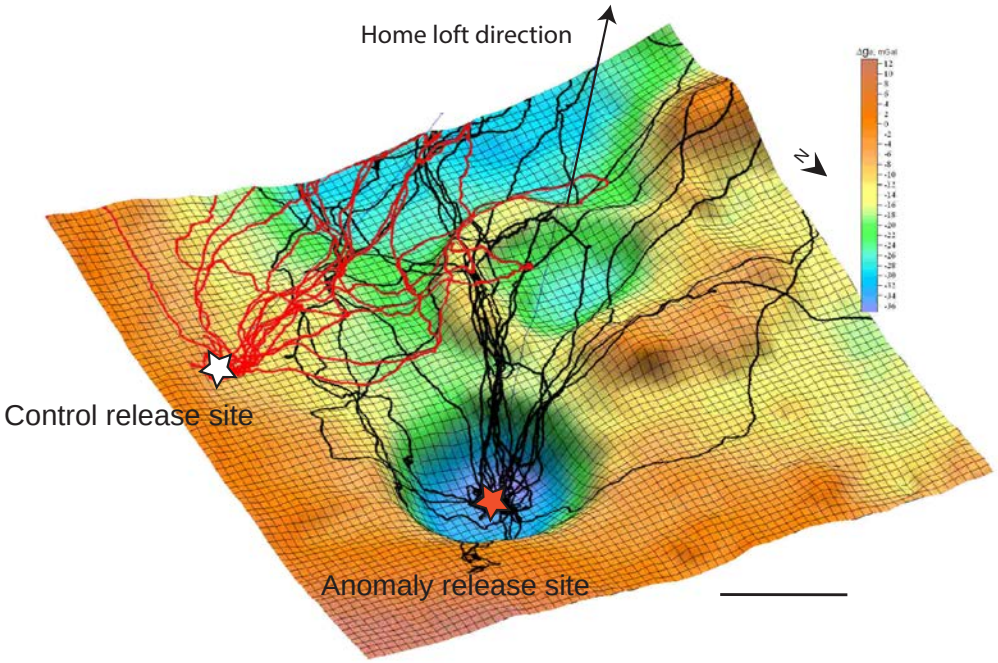

Fig. 3. The initial part of flight tracks of pigeons released from the centre of the gravity anomaly and from the control site. The flight tracks are superimposed on a 3D-gravimetric anomaly map showing gravity intensity differences. A steep level-change indicates a change in the horizontal gravity gradient. The red star is the release site within the anomaly. The white star is the control release site and the black arrow shows the home loft direction. The scale bar is 15 km.

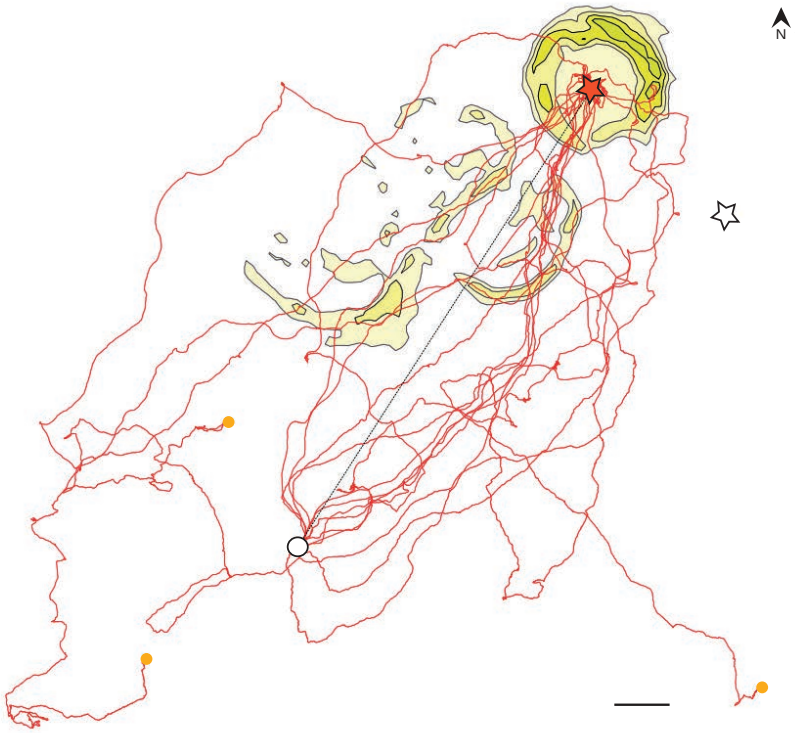

Fig. 4. Tracks of pigeons released from the centre of the gravity anomaly. The red star is the release site within the anomaly. The white star is the control release site and the white circle represents the home loft. The dotted line is the beeline from the anomaly release site to the home loft. 17 flight tracks are colored in red and superimposed on a scheme of a horizontal gravity gradient map of the Boltischka anomaly colored in yellow. The contour lines of the gravity anomaly are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (E = 20), middle (E = 30), dark (E = 40). 1 E = 0.1 mGal/km. Three tracks are disrupted, indicated with orange dots. The scale bar is 10 km.

Six out of 7 pigeons that flew out of the anomaly in the homeward direction, changed their course 5 km after crossing the border zone. The 6 pigeons turned to SSE for 15 km, from where two pigeons changed their course southward, three continued their SSE direction for another 20 km. There is one pigeon that aligned its course with the contour lines of the second arc-shaped anomaly, changing its heading from south to northwest and was later lost, north of the home loft (pigeon 451). When tracing the orientation of the group of pigeons that headed W-SW out of the anomaly, three of them kept a western direction also for 20 km until one of them turned southeast, crossing the arc-shaped anomaly while another pigeon adjusted its course every 20 km until it homed.

Figure 5 shows the flight tracks of the pigeons released from the control site. In general, the flight tracks conglomerate around the beeline from the release site to the home loft. There are two exceptions: one pigeon flew toward home but then passed the home area and turned north, ending 85 km north of the home loft. Another pigeon followed a second pigeon into the arc-shaped anomaly, returned to the control release site and then flew in easterly direction where it paused (Fig. 5, both tracks with orange points at the end).

The analysis of the closeness of the flight tracks to the beeline from the release site to the home loft revealed that the pigeons released from the centre of the gravity anomaly were dispersing widely with distances up to 55 km from the beeline (Fig. 6). The dispersal distances between the pigeons released at the gravity anomaly and those released at the control site were significantly different at distances 25, 35, 45 and 55 km from the release site (Mann-Whitney-U-test). As 8 pigeons were released from both places, an additional analysis of the dispersal distances of only 8 pigeons was performed with the Wilcoxon singed-rank test for paired data: the two pigeon-groups were significantly different at distances 45 and 65 km ($p < 0.05$) and almost significant at distances 55 and 75 km ($p = 0.055$) from the release site.

A comparison of the flight tracks of individual pigeons released at both sites is depicted in Figure 7 and 8. The numbers at the release site denote the order of release. Three pigeons aligned their flight paths to the second anomaly shaped like an arc, southwest of the circular gravity anomaly: pigeon 451 (Fig. 8B) flew along the arc and was disoriented afterward, pigeon 441 (Fig. 8C) flew along the arc when released from the control site and returned again along the arc of the anomaly and pigeon 418 (Fig. 7C) flew along the arc

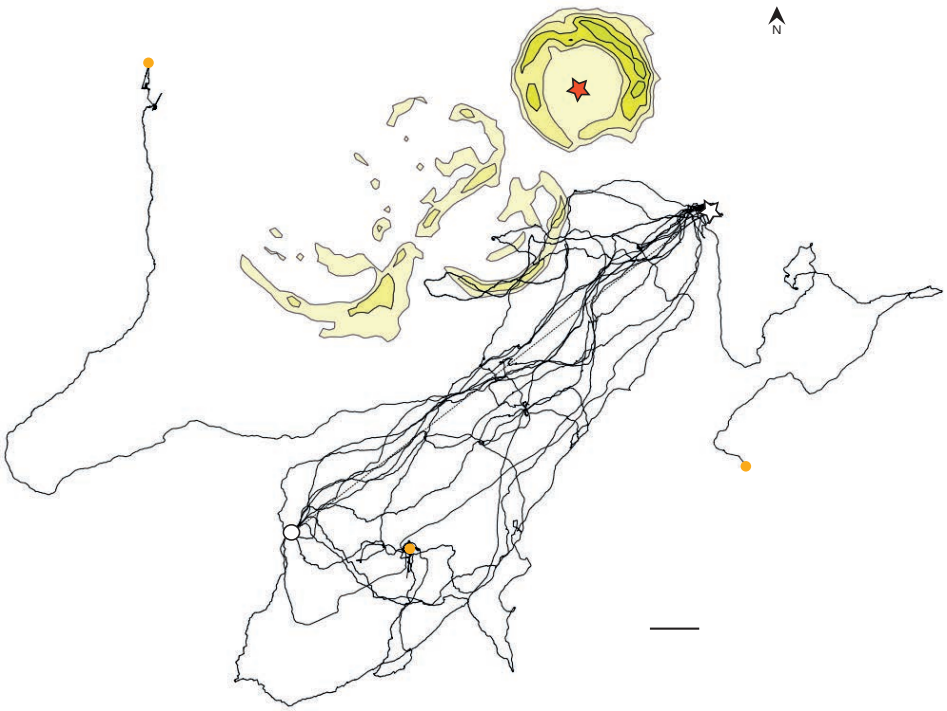

Fig. 5. Tracks of pigeons released at the control site. The red star is the release site within the anomaly. The white star is the control release site and the white circle represents the home loft. The dotted line is the beeline from the control release site to the home loft. 14 flight tracks are colored in black and superimposed on a scheme of a horizontal gravity gradient map of the Boltischka anomaly colored in yellow. The contour lines of the gravity anomaly are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (E = 20), middle (E = 30), dark (E = 40). 1 E = 0.1 mGal/km. Three tracks are disrupted, indicated with orange dots. The scale bar is 10 km.

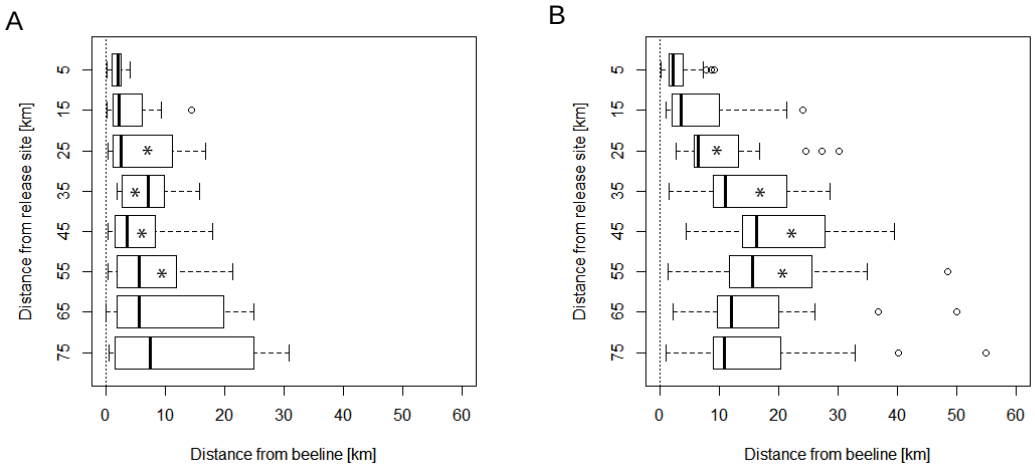

Fig. 6. The dispersal distances of the pigeons from the beeline release site-home loft. A) Distances of the C-pigeons from the beeline at 5 km steps. B) Distances of the A-pigeons from the beeline at 5 km steps. The values are absolute values, i.e. disregarding the side of the beeline. The box ranges show the upper and lower quartile with the median, and whiskers extend to the most extreme data point no more than 1,5x the interquartile range. Points outside the range are outliers. The stars indicate significant differences between the C- and the A-pigeons (Mann-Whitney U-test).

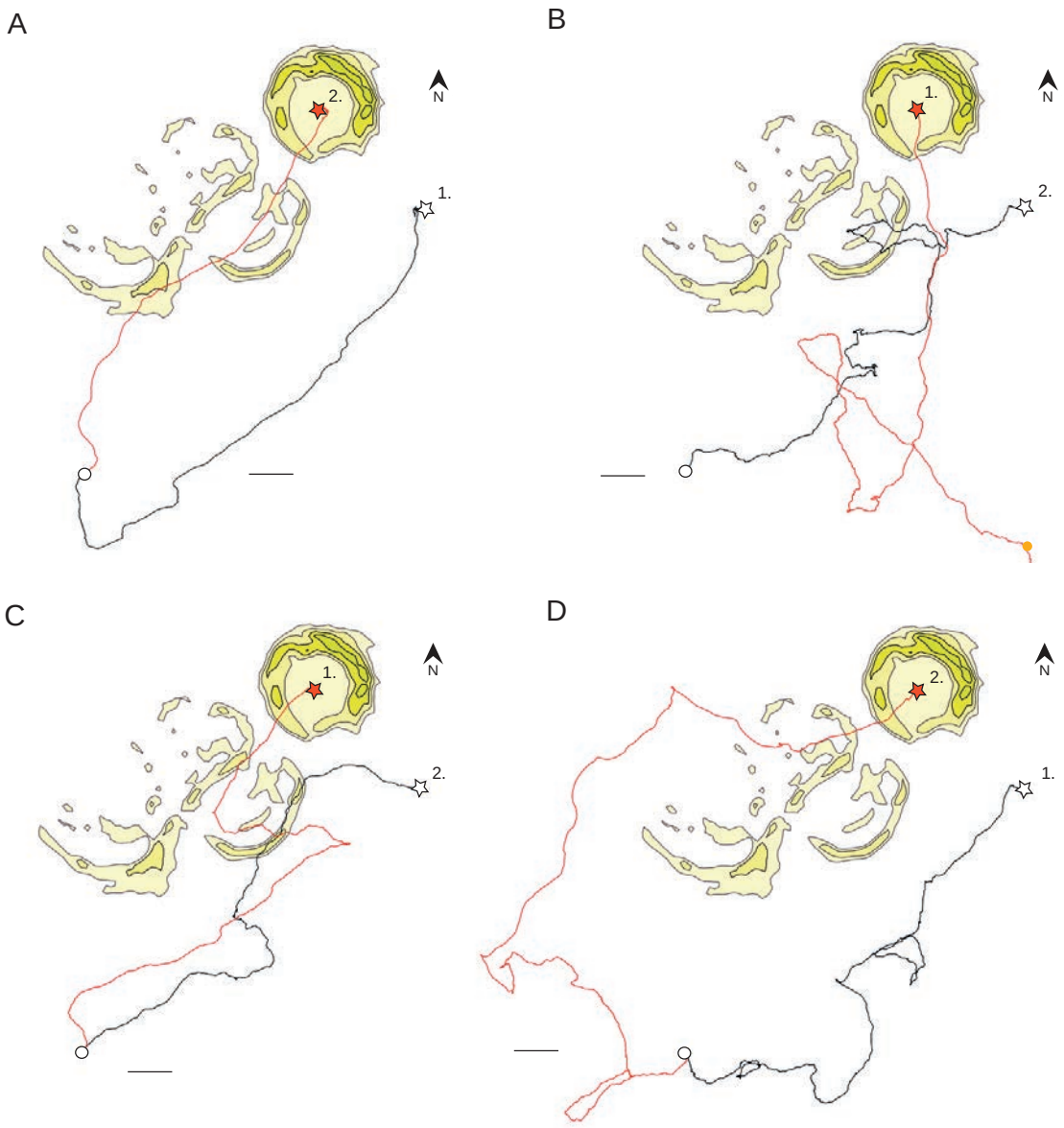

Fig. 7. Tracks of individual pigeons released from within the anomaly and from the control site. The red star is the release site within the anomaly. The white star is the control release site and the white circle represents the home loft. The numbers at the release sites indicate the order of releases, i.e. 1. means the pigeon was released first at this release site and second at the other site. The red tracks are pigeons released from within the anomaly, the black tracks are pigeons released from the control sites. A) Pigeon b26, B) pigeon b25, C) pigeon 418, D) pigeon 323. The tracks are superimposed on a scheme of a horizontal gravity gradient map of the Boltischka anomaly colored in yellow. The contour lines of the gravity anomaly are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (E = 20), middle (E = 30), dark (E = 40). 1 E = 0.1 mGal/km. The small orange dots indicate disrupted tracks. The scale bar is 10 km.

also when released from the control site, paused three times afterward and then corrected its course toward the home loft. Another pigeon kept its southwestern course steady for about 100 km until it circled, changed to the south, to approach the home loft from the opposite direction (Fig. 8D). This pigeon had an excellent return from the control site and it seems conceivable that it applied the same compass course from the anomaly site as it experienced 2 weeks before, when released from the control site. This finding is also astonishing because it implies that the pigeon remembered the previous flight course 2 weeks ago. Then, released behind the anomaly, the pigeon flew initially in the correct homeward direction but in front of the arc-shaped anomaly, it turned to the west and returned to the loft a few days later.

The quantitative analysis of all flight tracks did not show a significant difference in any of the track parameters of pigeons released within the anomaly and at the control site. In general, all pigeons were moderately homeward oriented (path ef), flying tortuous paths and taking rests during the journey home. The values of the flight track parameters of pigeons released within the anomaly were: path lin = 94±1.9%,

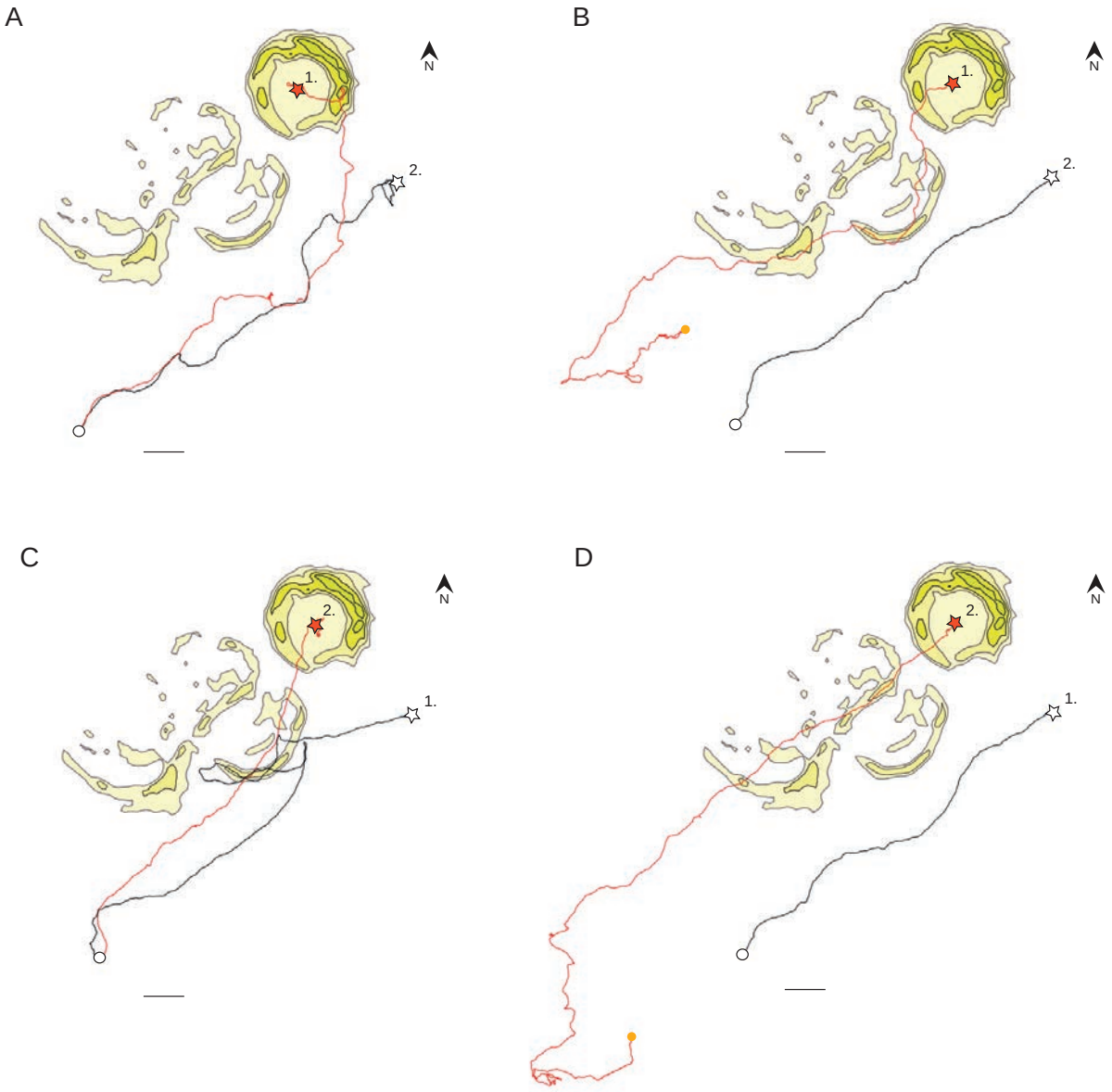

Fig. 8. Tracks of Individual pigeons released from within the anomaly and from the control site. The red star is the release site within the anomaly. The white star is the control release site and the white circle represents the home loft. The numbers at the release sites indicate the order of releases, i.e. 1. means the pigeon was released first at this release site and second at the other site. The red tracks are pigeons released from within the anomaly, the black tracks are pigeons released from the control sites. A) Pigeon 311, B) pigeon 451, C) pigeon 441, D) pigeon b20. The tracks are superimposed on a scheme of a horizontal gravity gradient map of the Boltischka anomaly colored in yellow. The contour lines of the gravity anomaly are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (E = 20), middle (E = 30), dark (E = 40). 1 E = 0.1 mGal/km. The small orange dots indicate disrupted tracks. The scale bar is 10 km.

path ef = 58±17.0%, home ef = 65±13.5%, and GPS speed = 68±7.2 km/h. The values of the flight track parameters of pigeons released at the control release site were: path lin = 94±3.0%, path ef = 62±16.5%, home ef = 63±16.9 km/h, and GPS speed = 65±5.5 km/h.

Releases behind the gravity anomaly

The pigeons released 4 km behind the anomaly were initially all very well homeward oriented (Fig. 9B). They crossed the anomaly at the strongest gradient, three of them flew across the gravity anomaly in the home loft direction and one pigeon headed south (Fig. 9A). Three pigeons continued the homeward course until they hit the second border zone where two pigeons deviated southerly and one pigeon turned to the west which were also the two main flight directions we observed in the releases from within the anomaly. One pigeon already changed its flight course when hitting the lower border of the anomaly, flying to the west, returning to the arc-shaped anomalies and then homing successfully. Pigeon b20 flew more southerly than before when released within the anomaly, yet again in a wrong direction and overshooting the loft,

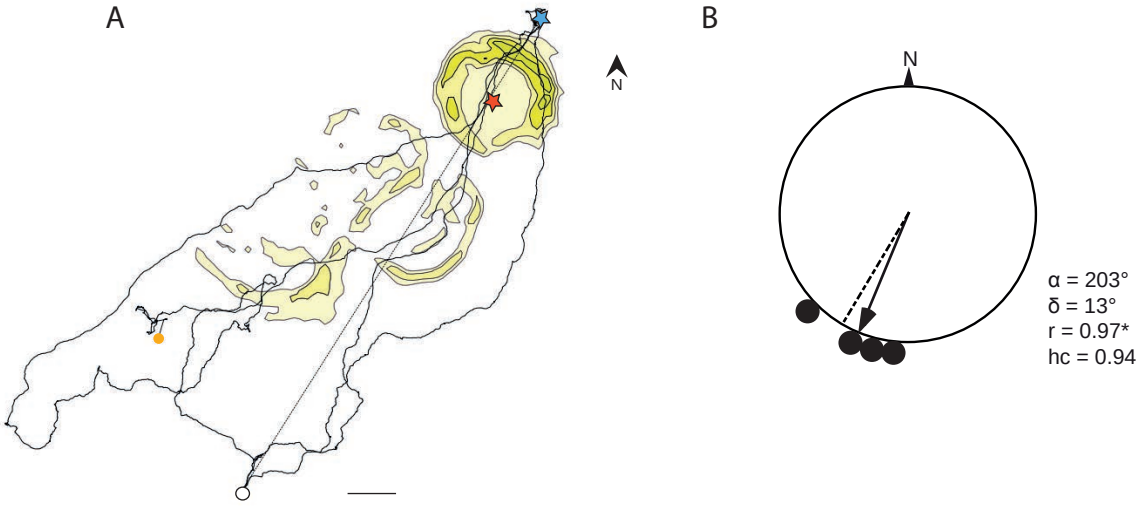

Fig. 9. Individual pigeons released behind the anomaly. All four pigeons (b31, b20, b26, b25) were previously released from the control site and from within the anomaly. A) The red star is the release site within the anomaly. The blue star is the release site behind the anomaly and the white circle represents the home loft. The flight tracks are superimposed on a scheme of a horizontal gravity gradient map of the Boltischka anomaly colored in yellow. The contour lines of the gravity anomaly are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (E = 20), middle (E = 30), dark (E = 40). 1 E = 0.1 mGal/km. The small orange dot indicates a disrupted track. The scale bar is 10 km. B) The position of the pigeons at 2 km from the release site. α is the mean vanishing vector, δ is the deviation of the mean vanishing bearing from the homeward direction, r is the mean vanishing vector and hc is the homeward component. According to the Rayleigh-test, r is significant, indicated with * = $p<0.05$.

but then paused northwest of the home loft only to return home a few days later (Fig. 9A, track with orange point at the end).

Discussion

The pigeons' initial orientation, 2 km distant from the anomaly release site, was scattered and was different to the orientation of the control pigeons. However, soon after but still within the circular anomaly, the pigeons oriented homeward and did not differ in their orientation as compared to the control pigeons. The second prediction was also confirmed: pigeons that crossed the anomaly showed changes in their flight direction and dispersed over great distances. However, both groups showed a substantial number of losses. Thus, the data sample is (conservatively) biased since there is no information about the lost pigeons.

Initial orientation

The pigeons seemed to be slightly disturbed when being released within the anomaly, vanishing to the northwest, southwest and to the east. Within the circular gravity anomaly there were only minimal changes in the horizontal gravity gradient. The disorientation could be an effect attributed to specificities of the release site. Alternatively, the pigeons might have sensed the circular gravity anomaly at a distance. Whatever reason, after 5 km, the disturbance was overcome and the pigeons showed a homeward orientation. In comparison, the vanishing bearings of the control pigeons were extraordinary aligned to the homeward direction. As a consequence, both groups did not differ in their orientation toward home.

Crossing the border zone of the gravity anomaly

Most pigeons crossed the border zone in a very direct course with no apparent directional changes. But there are two pigeons, both of them flying to the south, that flew a large circle exactly in the border zone. Flying circles is considered to show an insecurity of the bird about its orientation and by flying a circle it is suggested that the bird determines its position again. The same interpretation is applied to a similar behavior, turning around, which is observed in a variety of other animals such as ants (Wehner et al., 1979) and dung beetles (Baird et al., 2012).

The flight tracks after the anomaly: impact of the second gravity anomaly

A considerable number of pigeons changed their flight course after crossing the border zone of the circular gravity anomaly. Almost all pigeons were quite well aligned to the homeward direction 15 km from the centre of the anomaly. After crossing the anomaly, they started to diverge in both directions away from the beeline "release site-home loft". Furthermore, when encountering the second arc-shaped anomalies, their deviations increased, leading to a maximal mean distance of 19 km from the beeline "release site-home

loft". Some pigeons aligned their flight course to the contour lines of the second arc-shaped anomaly.

Releases behind the gravity anomaly

The pigeons released behind the anomaly had all been released previously within the anomaly and at the control site. The release site behind the anomaly exposed them to crossing two border zones, the first one with the greatest horizontal gravity gradient. The pigeons' initial orientation was strongly homeward-aligned. Thus, their position-determination and compass-setting was not impaired. However, after they had crossed the circular anomaly, they diverged and interestingly, they deviated very similar to the overall pattern of the tracks released from the centre of the anomaly: either more to the west or then, more to the south.

In general, it is rather unusual that pigeons, once heading toward the correct homeward direction change their course completely, deviating for long distances. The pigeons, having encountered the gravity anomaly, might have corrected their flight course wrongly, leading to a dispersed behavior, flying away from a direct course in the middle part of the journey. Coming closer to home, possibly sensing the distance flown, they determine their position again and home successfully. This comparison might also explain why both pigeon groups did not differ in their overall performance, i.e. the comparison of flight track parameters: the pigeons released from within the anomaly were still well aligned 15 km apart from the release site and also at the end of their journey.

The greatest difference between both pigeon groups was the dispersal pattern in the middle part of the journey, also influenced by the second arc-shaped anomaly. Another important point is that we lost quite a number of birds of which we do not have any information on their flight behavior and thus, the data is biased toward pigeons that did home successfully. Thus, it might well be that the complex gravity anomalies had more deleterious effects on pigeon navigation than suggested by the tracks of the successful homers.

Conclusions

1. As expected by the theory, releasing the pigeons from the centre of the anomaly had no strong impact on their vanishing bearings. This implies that the birds had a normal position-determination and compass setting toward their home loft when released within and behind the Boltischka circular gravity anomaly. Most pigeons did not change their flight course immediately while crossing the anomaly but only later, either by recalculating their position due to the unexpectedly changed gravity gradients, or because they faced a second anomaly showing both positive and negative values of the vertical component of the gravity vector, entailing quickly changing gradients in their flight direction.

2. Most of the tracks diverging after passing the border zones of the gravity anomaly suggest a wrong setting of compass directions, leading them farther away from the ideal line and overshooting the loft.

3. A lower number of GPS tracks shows clear alignment of flight paths along the contours of the second gravity anomaly, and few tracks altered their direction within the border zone of the circular anomaly. As the geomagnetic variation in these zones was very low, in the range of normal zones, these observations strongly suggest that some pigeons can also show a strategy of following gravity gradients temporarily.

4. We conclude tentatively that pigeons appear to adopt predominantly a map-and-compass strategy based on the gravity situation at the release site, but seem to be alert to changes in gravity gradients for about 5-10 km after the release. In this phase, anomalies appear to induce new and often inappropriate compass directions.

5. The high number of pigeons lost also from control sites implies that future studies should refrain from control releases in the vicinity of gravity anomalies, unless it becomes possible to track lost pigeons.

6. If the gravity-based map-and-compass theory of bird navigation is correct, then releases from the border zone of the Boltishka anomaly that show maximal gravity gradients should entail strong and persisting directional changes and loss of birds.

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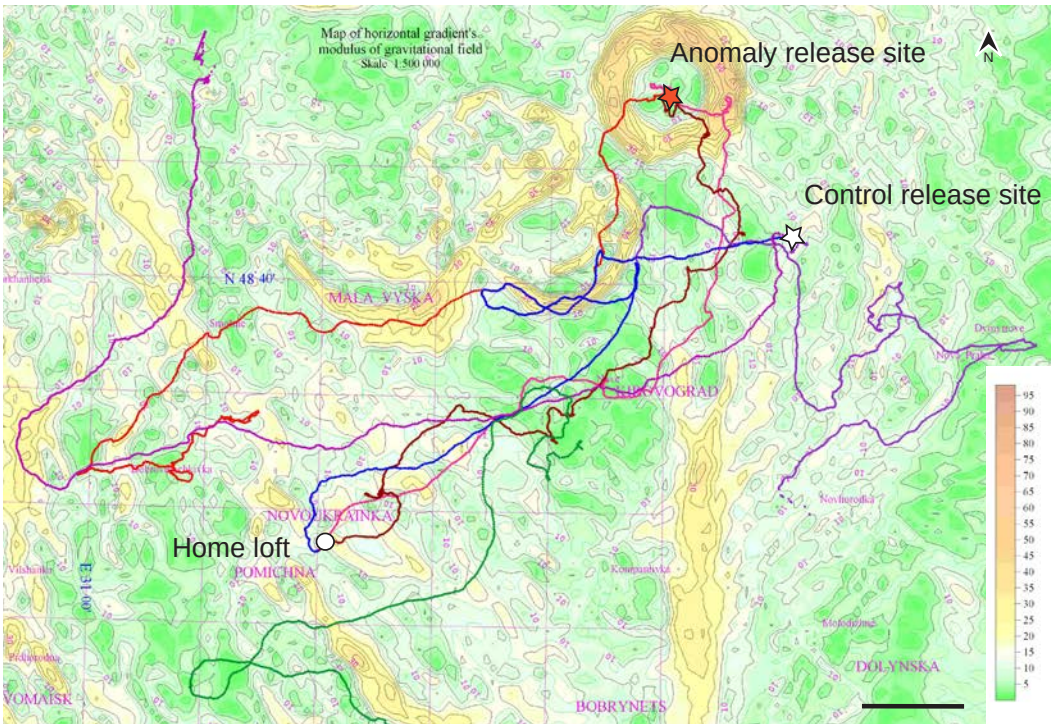

Fig. S1. Map depicting gravity anomalies of the test region. A random selection of 7 pigeons flying from the anomaly, indicated with at red star, and the control site, indicated with a white star. The white point is the home loft. The map shows the horizontal gravity gradient (0-95 E = Eötvös). The scale bar is 20 km.

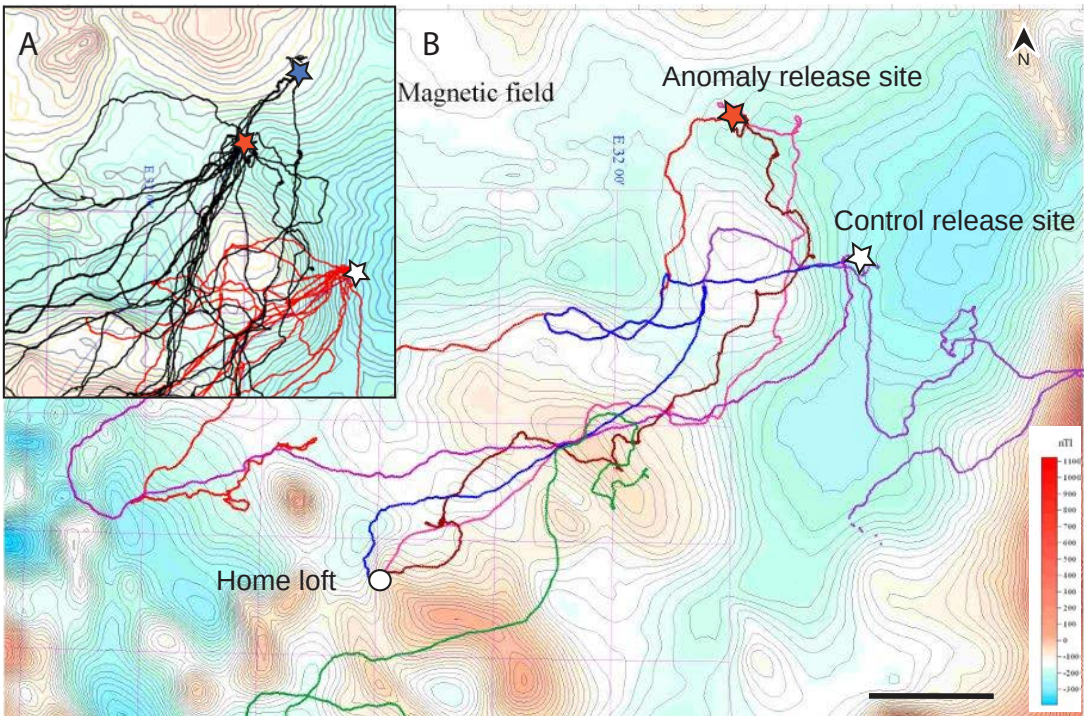

Fig. S2. Map depicting magnetic anomalies of the test region. A) Black tracks are flight tracks from pigeons released within (red star) and behind the anomaly (blue star), red tracks are flight tracks of pigeons released at the control site (white star). The interval of the contour lines are 5 nT. B) A random selection of 7 pigeons flying from the anomaly, indicated with at red star, and the control site, indicated with a white star. The white point is the home loft. The map shows magnetic intensities in nT = nanoTesla (-300-1100). The interval of the contour lines are 10 nT. The scale bar is 20 km.

Discussion

The aims of this thesis were to a satisfactorily extent fulfilled. We were able to answer our hypothetical questions and meet the predictions made, using our unique design of experiments with homing pigeons and the observation of flight tracks by means of GPS loggers. The collected data and methodological analysis of the flight tracks were discussed in detail in the specific chapters. Thus we will concentrate in this section on elaborating general findings and clarifying conceptual issues in consideration of the mentioned theories.

Homing pigeons have a cognitive map

In our first project, we intended to investigate whether homing pigeons can memorize large-scale navigational maps beyond their home range. In animal navigation research, a navigational map is usually being defined as a mental representation of memorized locations. A crucial distinction is the application of the map: whether it is used in previously visited areas or extendable to more distant and unknown areas. The application of a familiar map is generally referred to a mosaic map (Papi et al., 1972), a familiar area map (Baker, 1978) or a topographical map (Wallraff, 1988). The application of an extendable map is named a grid or gradient map (Wallraff, 1991a) where the home values and gradients in the home area are memorized. There is no doubt that pigeons can memorize spatial relations of familiar cues such as landmarks or olfactory sources with their home loft to form a cognitive map. However, until now, it has not experimentally been clarified whether pigeons can determine their position and retrieve the position of multiple memorized locations in an unfamiliar area.

In our first experiment, we let pigeons choose between two goals in an unfamiliar area. The results showed that the pigeons determined their target direction at the beginning of their journey and thus had knowledge of their position and its relation to two other positions, which is the definition of a cognitive map. This is the first experimental evidence that pigeons have a mental representation of positions also in unfamiliar areas.

The implication of having a cognitive map is being able to determine a position and thus relates to the first step of the map-and-compass strategy proposed by Kramer in 1953. Our finding is of

significant importance because it excludes the restriction that pigeons could home by less cognitive demanding strategies such as route-based navigation. Route-based navigational mechanisms are path integration, piloting and beaconing (sensu Able, 2001) and do not require a map. However, despite of having a map, pigeons are also able to switch to less demanding strategies when their implementation is sufficient to lead them home. For example, when encountering a familiar highway, they might follow it since the pigeons have memorized that the highway leads them toward home as shown in a study by Lipp et al. (2004).

The finding that pigeons have a cognitive map does not, however, elucidate the nature of the underlying mechanism of position-determination. Until now, there is only one concept for position-sensing in distant regions: the grid or gradient map hypothesis. The grid map is built with at least two intersecting coordinates that vary systematically, also called gradients. Such gradients can be formed by olfactory, geophysical or any other cues that have increasing or decreasing values. However, the gradient map hypothesis is often confused with a simpler gradient strategy, i.e. following gradients that emanate from a goal. This does not require any position-determination and belongs to the route-based navigational strategies sensu Able.

A somewhat remote explanation for the findings of our study is a physiologically induced target-orientation. The pigeons associated the second target, the food loft, with receiving food. Thus, whenever their level of hunger increased above a threshold, the position of the food loft could have dominated as a target location. Therefore, at the release site, the pigeons that had a hunger level above the threshold would have only one target in mind, resembling a one-target orientation without an active decision-making process. The pigeons that were fed, had a hunger level below the threshold and thus, the associated location with satiation was their home loft. Practically, this alternative explanation is questionable as it implies that pigeons orient exclusively according to their physiological condition in a robot-like fashion and would not be capable to react to external influences.

An experiment addressing this alternative explanation could be done by releasing hungry and satiated pigeons from a release site near the home loft at sunset. The food loft would be considerably further away and if pigeons chose to fly there, they would be flying into the dark. Pigeons do not like to fly at night and therefore, should prefer to home quickly and seek shelter in their home loft. Even if only a few hungry pigeons chose to fly home, it would invalidate the physiological-induced alternative hypothesis. In addition, if released in an unfamiliar area, the experiment could show that pigeons

have a sense of distance. For such an experiment, one target, the home loft, would suffice and pigeons could be released at increasing distances from the home loft. Pigeons that would fly into the dark because of a great distance to the home loft might stay at the release site and overnight in a nearby tree. This assumption is based on the repeated observations of pigeon fanciers, that pigeons released in the evening will not depart unless the loft is close. Thus, both experiments could validate the use of a cognitive map as distance is inherent in a spatial map. Until now, only a laboratory investigation of spatial orientation could confirm distance-estimation of homing pigeons (Gibson et al., 2012).

Homing pigeons are influenced by gravity anomalies

In our second project, we investigated whether gravity anomalies disturb the orientation process of homing pigeons and thus convey support for the gravity vector theory. The essence of the theory is that birds become imprinted to the local gravity vector early in life. Thus, when a bird flies away from its home location, the angular difference between the memorized home gravity vector and the locally perceived gravity vector increases. The comparison of two vectors pointing to the centre of the earth allows to construct on the surface of the globe a polar coordinate system, defining the position of the home loft by direction and distance only. As the gravity vector is not easily manipulated experimentally, we tested predictions of the gravity vector hypothesis with homing pigeons flying over strong gravity anomalies and with homing pigeons that were reared within gravity anomalies.

This is the first report of investigating homing pigeons crossing strong gravity anomalies by means of GPS. The conducted studies are also the first to investigate the effect of the horizontal gravity gradient on pigeon orientation. Until now, studies have dealt only with the initial behavior of homing pigeons flying from within a gravity anomaly with traditional estimation of vanishing bearings and the arrival time (Dornfeldt, 1991) and with radio transmitters (Lednor et al., 1984). These studies are limited inasmuch as they lack precise information on the flight behavior of the pigeons and they released the pigeons within an anomaly without having information on the gravity gradient. Kanevksyi was the first to let pigeons cross a strong gravity anomaly and could relate the observed changes in the flight paths with changes in the EEG (Kanevskyi et al, 1984).

In the first experiment in Ukraine, we exposed pigeons to different home areas with different gravity gradients to examine whether the birth location and thus the memorized home vector affects the orientation at a distant release site. We predicted that the pigeons would orient differently

according to the gravity gradient they grew up with. The predictions were confirmed but the flight performance of one group of pigeons was unexpectedly poor. Those pigeons reared outside the main anomaly but on a steep local gravity gradient showed also no directedness in the last training test. The steep gravity gradient at the home loft could account for the observed flight behavior but alternatively, the location of the loft in the neighborhood of the strong Bandurove gravity anomaly might have disturbed the formation of a navigational map, because free-flying birds would experience conflicting gravitational information. Generally, free-flying homing pigeons do not venture far beyond the loft, maximally about 1 km as evidenced by GPS-tracking (unpublished observations). The second group of pigeons showed deviations in their flight paths when crossing the anomaly and these results also corresponded to the prediction made.

In the second experiment in Ukraine, we reared pigeons in normal gravity conditions and released them within and behind a circular gravity anomaly. We predicted that the pigeons would change their flight direction after crossing the anomaly which most of the pigeons did. In addition, their flight behavior was also affected by a second gravity anomaly they encountered on their way home. It is remarkable how the pigeons released from within the anomaly changed their flight course after crossing the anomaly and stayed on that deviating course for a considerable time.

Gravity anomalies often coincide with magnetic anomalies if changes in underground densities are caused by deposit of magnetic minerals. There were magnetic anomalies in the area of the gravity anomaly in the first experiment but they did not coincide locally with gravity anomalies. However, for the first study, we cannot exclude firmly a possible effect of magnetic anomalies on the pigeons' behavior. In the second experiment, the gravity anomaly was formed by a meteorite impact and did not show any abnormal magnetic values. Therefore, the observed flight behavior cannot be attributed to a disturbing influence of magnetic anomalies.

Altogether, the results strongly indicate that gravity anomalies affect pigeon homing and specifically, that the horizontal gravity gradient might be the crucial factor. As a consequence, the results also support the gravity vector theory.

Experimentally, the theory might also be tested in the laboratory with a discrimination learning task in a setting with large objects of different mass density. Objects with heavy minerals are able to tilt the perceived gravity vector and could elicit a different behavior of the pigeons than objects with average density. The mineral should be non-magnetic and the decrease of mass attraction over

distance should be taken into consideration. The outcome of such a study could significantly amplify our findings of the influence of gravity anomalies on pigeon orientation.

The bird's monitoring of its flight course

A general unanswered aspect of animal navigation is the time interval of positional updates. How often does a bird update its course during flight? If we assume that on one extreme the map-and-compass strategy would imply that a bird determines its position at the release site and afterward heads off along the set compass course, it would not need to change its course until it reaches home. On the other extreme, a gradient-following strategy would mean that the bird would update its course according to the momentarily perceived external values and thus the flight course would be adjusted in very short intervals or even continuously. In the Italian study with pigeons being released behind a lake, it is apparent that the birds set their compass course at the release site but had to circumvent the lake and later aligned their course to the previously determined compass setting. Surprisingly, they did not adjust to a new compass setting that would have led them to a more direct approach toward home. These results indicate that the pigeons memorized the compass they set at the beginning of their journey. When investigating the flight tracks of the pigeons released within the circular gravity anomaly it is also apparent how some birds seem to adjust their flight course every 10 km, other birds flew in a 'wrong' bearing for over 50 km, implying individual differences in the timing of course corrections.

There is another aspect to be considered: the sensibility of individual birds toward external stimuli. There appear to be birds that are either highly sensible to external influences or they have simply a low threshold of reactivity, i.e. they respond very quickly to numerous stimuli. We have observed pigeons that find their way home but instead of flying a compass course, they are often distracted by landscape features such as rivers, canopies and agricultural roads marking borders of farm land, which they follow for some time before correcting the flight direction. Other pigeons fly a straight compass-course regardless of the topography. The same mechanisms may apply to pigeons flying over gravity gradients: a pigeon can set its compass course at the release site and follow it but then encounters a steep gravity gradient which it senses, causing it to use the new information for computing a different home bearing. In that case, pigeons would change their flight course after crossing a steep gravity gradient. However, a pigeon might sense the change in the gravity vector but ignore the information and continue its compass course. In that case, we would not observe a change in its

flight path. A third possibility is, that a bird is not able to sense the change in the gravity vector and therefore is not affected by it.

To summarize, the interval of positional updates and the sensibility to external information is crucial for a thorough interpretation of the observed behavior of a navigating animal. The results of our data suggest that pigeons set the compass at the beginning of their journey and that there are individual differences as to how often they adjust their flight course. There is also a striking difference between the flight behavior of the pigeons in the cognitive map-experiment and in the experiments with gravity anomalies. In the cognitive map-experiment, the birds adjusted their course as soon as they circumvented the lake to the previously set compass course. In the Boltishka (circular gravity anomaly) experiment, the birds first set a correct compass course toward home but then corrected the course after crossing the anomaly into a 'wrong' course and followed that course for 30 km, leading them astray. This observation has two conclusions: first, most of the birds sensed the gravity anomaly and used the information to update their compass setting. The birds then followed the novel computed course for 10 to 50 km according to their individual monitoring of their flight course. Second, most of the birds reacted to the gravity anomaly and thus, an external information influenced them to update their position. Therefore, a bird can have its individual monitoring time interval but can also update its position according to information from the environment in a flexible manner. It would be promising if future research could address this topic as it influences the course of a navigating animal. We suggest an analysis of pigeon homing tracks, most ideally with multiple tracks of individual birds alike that might show a recurrent pattern of course changes. The individual monitoring time interval might also change in function of age, flight experience or home location. The findings of such an experiment might shed light onto underlying navigational strategies and which of them are preferred in what habitat.

Gavity-based navigation: comparison with other map models

The gravity vector hypothesis is based on a polar coordinate system derived from two vectors pointing toward the centre of the earth, resulting in direction and distance to a point characterized by the memorized gravity vector. Therefore, the model comprises positional and directional information and thus would not need any other information. However, such an exclusive use is unlikely given the proven ability of pigeons to use multiple directional cues and the evidence of use of celestial cues in

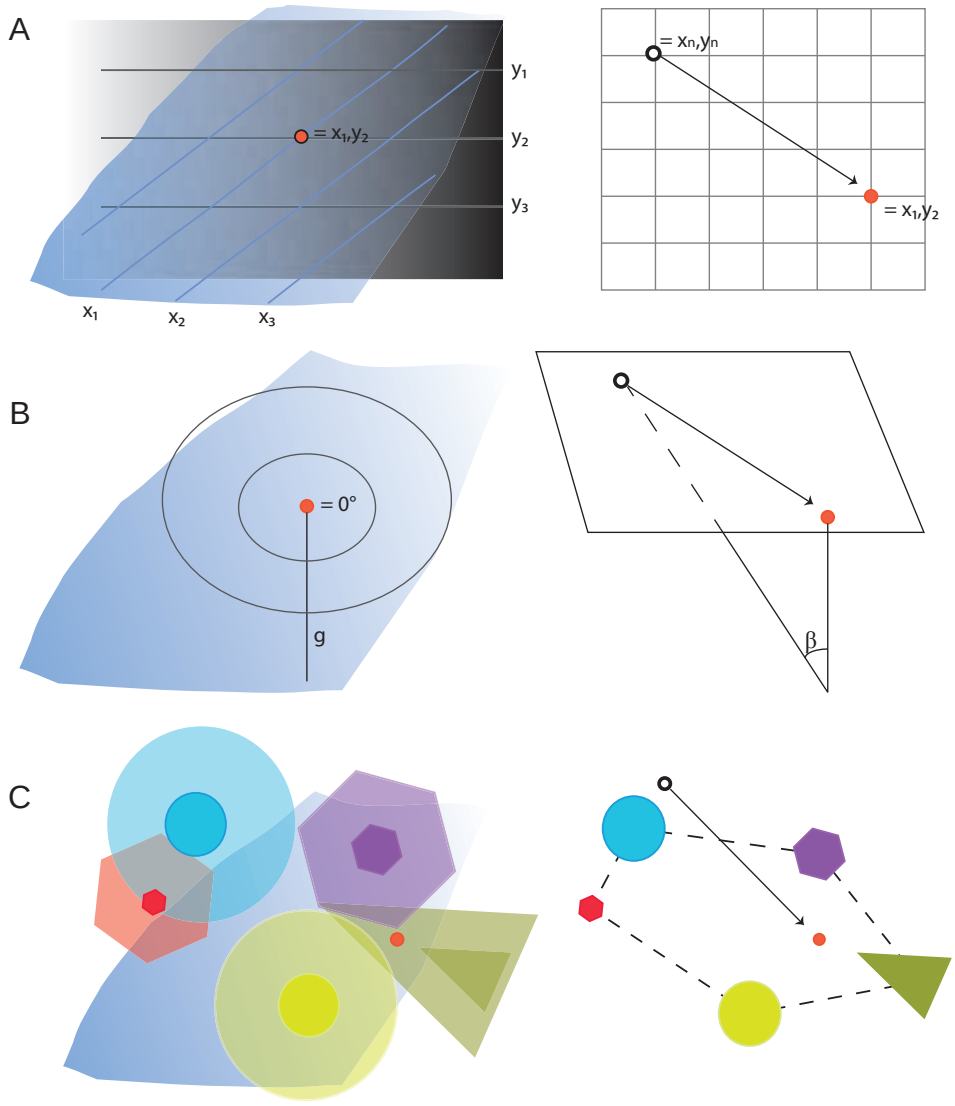

Fig. 1. Illustration of navigational map theories. The orange point depicts the bird's home location. The black-rimmed point depicts the bird's position after displacement. A) Grid map based on a minimum of two coordinats as gradients. The direction home is calculated by the difference of the perveiced values (x_n, y_n) with the home values (x_1, y_1). B) Gravity vector map based on the gravity vector g. The direction home on the surface of the polar coordinate system is defined by the angle β. C) Mosaic map based on emanating cues from environmental sources. The direction home is defined by comparing spatial relations or familiar sights of the cues.

migratory birds. It seems more likely that the gravity vector might function primarily as a position-finding mechanism. An indication for position-sensing is found in the experiment with pigeons reared on a gravity gradient: the pigeons memorized the direction of the gravity gradient at home and when released at a distant site, they flew first in that direction. In addition, incorrect calculation of the position might lead to prolonged disorientation or incorrect heading as the pigeons did not correct their course immediately but only very late, sometimes after overshooting the home area as evidenced in both gravity-related release studies. On the contrary, experiments on clock-shifted pigeons revealed that the pigeons would calculate the position of the sun wrongly and thus fly into a wrong direction

but mostly corrected their flight course very soon after. The quick recovery of the flight direction might illustrate that a miscalculation of the flight course due to a compass cue does not impair the orientation of the pigeons for a long time whereas a miscalculation of the flight course due to a wrong position-determination has greater implications resulting in prolonged misdirected flight courses.

As a position-finding mechanism, the difference of the locally perceived gravity vector to the memorized home vector gives information on the position of the bird and then, by referring to the azimuth of the sun and other available compass cues, it determines its heading toward home. The great advantage of such a system is that it only relies on the gravity vector and needs no grid of intersecting coordinates of the nature of geomagnetic and olfactory values that are spatially and temporarily highly variable. Another traditional problem with bi-coordinate surface maps is the lack of or scarce information about longitude. This problem is solved with the gravity-based polar coordinate system as it works theoretically at almost any point on the earth, leaving the choice of multiple directions home only from an antipode point on the globe.

An important issue on navigation is the range of an implemented map. The mosaic map suffices for a short range (10-30 km), a magnetic gradient or grid map is doubted to form a coherent and reliable map over great distances (Phillips et al., 2006) and thus might be more advantageous on a medium range scale (30-100 km). The gravity vector map would close a gap and offer a system of position-determination on a global scale with an accuracy independent of cardinal directions. However, we do not claim that it substitutes other navigational mechanisms. Given the evidence collected for this thesis, it appears, however, as the backbone of a long-range global navigation system which includes additional species-specific mechanisms depending on the ecological niche and navigational requirements.

Despite its advantages, the gravity vector theory also poses problems:

(i) It requires an extremely sensitive sensory system for assessing the vertical angle between the vertical components of the gravity vector. For example, in our latitudes, one degree in longitude corresponds to about 100 km. The sensitivity might be increased if the bird derives information from the horizontal component, but without knowledge of the brain processes involved in memorizing gravity vector information the differences appear still minimal. However, the same problem is faced by theories assuming magnetic grids. Walker et al. hypothesized that averaging the direction of magnetic

vectors from arrays of many small sensory units might provide highly accurate estimates of the real vector (2002). Thus, a similar principle could apply to the sensing of gravity vectors in the brain of a pigeon. Clearly, the sensitivity of the putative system will determine whether comparing gravity vectors might serve mainly in long-distance navigation. Nonetheless, it should be recalled that pigeons carrying frosted lenses and therefore being visually impaired, were able to find their home loft with a precision of about 500 m (Schmidt-Koenig et al., 1978). If such homing is based on geophysical parameters such as gravity or magnetism, the sensitivity of these system goes far beyond what we can imagine today.

(ii) The second problem is the stability of the actually sensed gravity vector during flight. When a pigeon flies a narrow circle or moves its head, it could perceive changes of the actual direction of the gravity vector. The problem can be solved in different ways. For example, by mechanisms providing conceptual stability of perception as it is the case for our visual system in which saccadic eye movements prevent the perception of a bouncing environment caused by our body movements. A second solution might be a preference for setting a compass course at the beginning of a birds' home journey which would then not be influenced by sensed fluctuations of the gravity vector during flight.

(iii) There is at present no information on where and how the memory for a gravity vector is processed and stored. It might derive from the otholithic system by averaging and integrating the local topography (visibility of the horizon) with the gravity vector at the birth place. Alternatively, one cannot exclude the presence of non-otholithic graviceptor systems. Experimentally, this would require to study brain activity in relation to small gravity-induced changes in pigeons without otholithic/vestibular systems. There is some evidence that non-otholithic graviception systems exist in pigeons, as shown in studies of labyrinthectomized pigeons still having righting reflexes (summarized in Saborowski, 2001) most likely based on graviceptive signals from the trunk. Likewise, honey bees can be trained to graviceptors providing different inputs (Markl, 1966). Thus, future neurobiological research must aim at identifying additional graviceptive systems, preferably by means of functional neuroanatomy in labyrinthectomized pigeons, followed by neurophysiological recordings in potential candidate structures.

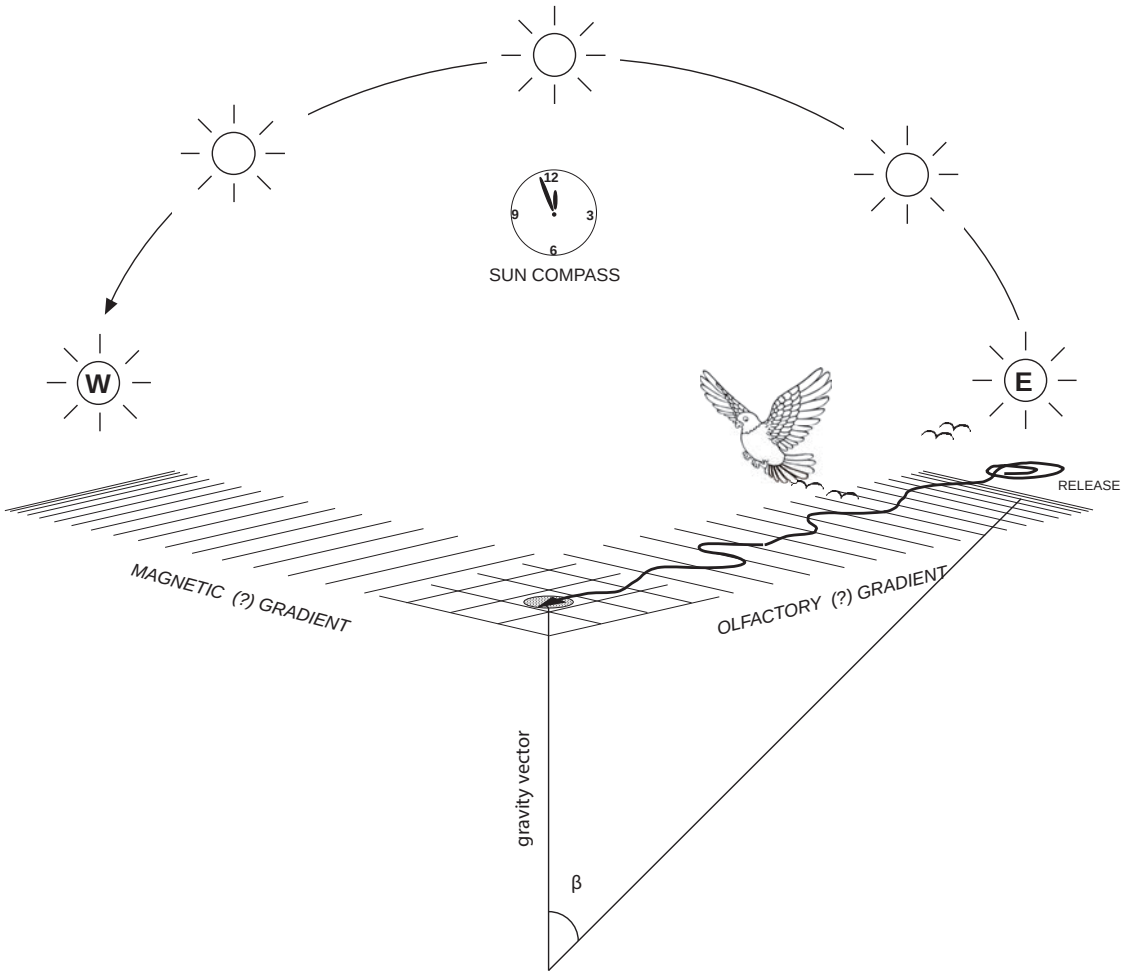

Fig. 2. Illustration of references for pigeon navigation. A sun compass, magnetic and olfactory gradients and the gravity vector are depicted. Courtesy of Prof. H.-P. Lipp, modified [18].

Overall conclusions

The findings of this thesis add valuable information to the knowledge of pigeon homing and navigation by confirming established theories and by verifying a novel navigational theory.

The main findings are:

1) Homing pigeons used a cognitive map in unfamiliar areas relating their own position not only to home but also to other learned targets.

2) Homing pigeons used a map-and-compass strategy to navigate home. However, the use of other navigational strategies is thereby not excluded.

3) Homing pigeons appeared to update their flight course in response to external stimuli and presumably according to individually set time intervals.

4) The orientation of homing pigeons was disturbed by gravity anomalies. They reacted to changes in the horizontal gravity gradient, both by setting inappropriate new home bearings or temporary changes of the flight course.

5) The predictions of Kanevskyi's gravity vector hypothesis were thus met. Although the data do not prove the hypothesis itself, it appears as the only theory that can explain the results and make correct predictions. Therefore, it is justified to assume that pigeons use gravity-based navigation strategies by comparing actual and memorized gravity vectors, which provides azimuth and distance to home (or another memorized place) on a global scale, supplemented by a flexible use of diverse compass systems.

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Publications

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Sommer, S., Weibel, D., Blaser, N., Furrer, A., Wenzler, N. E., Rössler, W., Wehner, R. (2013). Chemical recruitment in a thermophilic desert ant, *Ocymyrmex robustior*. *J. Comp. Physiol. A* 1-12.

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International Conferences

04/13 BIONAV/RIN13, Royal Institute of Navigation conference, Royal Holloway College, Egham, UK

06/12 ABS, Animal Behavior Society Annual Meeting, University of New Mexico, Albuquerque
Presentation: "Altered homing orientation of pigeons raised within and outside a gravitational anomaly"

07/12 ECBB, European Congress on Behavioural Biology, University of Duisburg-Essen

07/12 ZNZ Symposium, ETH Zurich, Poster

04/11 RIN, Royal Institute of Navigation conference, University of Reading, UK
Presentation: "Testing cognitive navigation: Homing pigeons fly to two different goals"

09/10 ZNZ Symposium, ETH Zurich, Poster

03/09 European Science Foundation COMPCOG expert discussion workshop "large-scale spatial cognition in birds and mammals", Testa di Lepre, Italy

Working & Studying abroad

07/12 Netherlands, University of Amsterdam: Summer Course 'Animal Movement Analysis'

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Publicity

Swiss radio "With the Ukrainian homing pigeons" 23/07/2011
Documentary of my PhD project in Ukraine on radio DRS2
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University film "Graduate Campus" 03/2012
A short documentary of my PhD thesis on the website of university of Zurich
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Swiss newspaper "The mysterious flight of the pigeon", 22/03/2012
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12/06 - 02/09	Assistant & analyst at Private Equity firm, Alpha Associates AG, Zurich
04/06 - 09/07	Ranger of a natural protected area, Greifenseestiftung, Zurich
01/03 - 05/07	Service staff part-time, Foodpoint AG, Zurich
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Computer skills

Microsoft Office	Word, Excel, Powerpoint, Outlook
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Statistical programs	SPSS, R, Oriana
GPS-relevant programs	Wintrack, QGIS, GoogleEarth Pro

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German	Mother tongue
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French	Oral & written skills good
Russian	Beginner level
Italian	Beginner level